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A Revision of the Reindeer and Caribou, Genus Rangifer

by A. W. F. Banfield

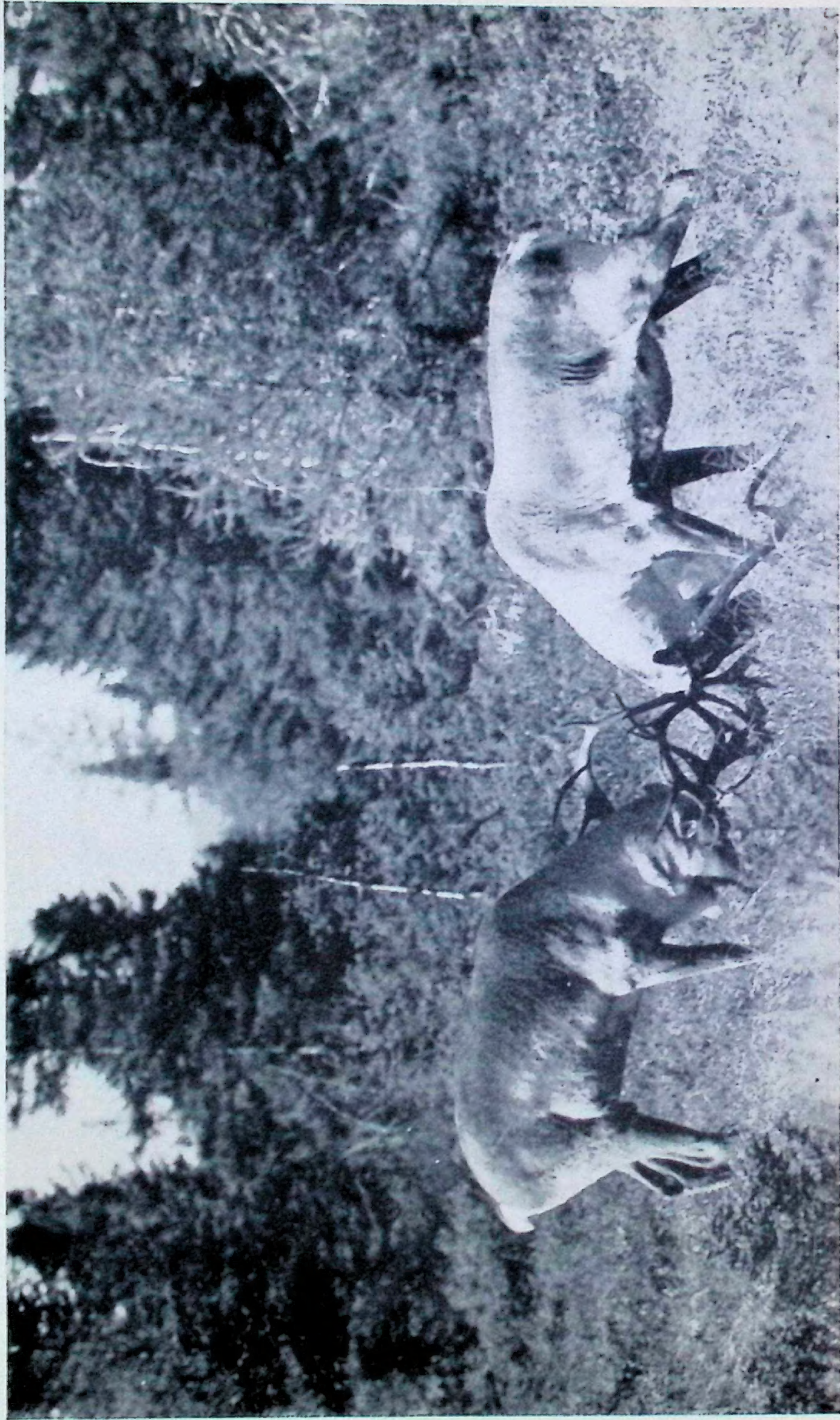
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Two Newfoundland caribou bulls sparring

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A REVISION OF THE REINDEER AND CARIBOU,
GENUS *RANGIFER*

by
A. W. F. Banfield

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A REVISION OF THE REINDEER AND CARIBOU, GENUS *RANGIFER*

INTRODUCTION

The history of the reindeer, or caribou, is of special interest because it is interwoven with the history of our own species in the Holarctic Region. Generally speaking, both appeared contemporaneously after the middle of the Pleistocene Epoch. Reindeer were rare in the mid-Pleistocene but became a dominant indicator of the cooler phases of the late Pleistocene of Europe. Abundant cave drawings of reindeer in the Dordogne valley of France and in Altamira in Spain indicated that reindeer served as a mainstay in the Palaeolithic cultures of our European ancestors. Caribou served the same vital role in the economies of arctic Eskimos and boreal Indians in the New World right up to recent times.

Originally, reindeer and caribou served as the basis of arctic and sub-arctic primitive hunting cultures in the Old World and in the New. The domestication of the reindeer occurred in northern Asia and subsequently spread to northern Europe and to western North America at the beginning of this century. This industry has greatly increased the economic importance of the species in modern times.

Although a great deal is known of the evolution and differentiation of man, relatively little of these processes is known of the reindeer. This hiatus in knowledge is largely the result of a lack of understanding of the taxonomic relationships between the living populations of reindeer and caribou. To this fact must be added the absence of a thorough analysis of the Quaternary reindeer remains.

It is appropriate that this study should be published in 1961, thirty years after the first complete revision of the genus by Jacobi (1931). During that period important developments have occurred in the understanding of the mechanics of evolution and in taxonomic procedures. Notwithstanding Jacobi's revision, the taxonomic relationships of the North American caribou populations were generally accepted as chaotic. The Eurasian situation was more clearly understood through the studies of the Russian mammalogists Flerov (1933 and 1952) and Sokolov (1937 and 1959).

Previous revisions had been conducted by the comparison of individual specimens or small series from distant localities. Often the comparisons were based on antler formation, a characteristic known to be highly variable and subject to nutritional level, or upon inadequate comparisons of skins taken at different seasons. Modern trends in taxonomy have laid less emphasis on the comparison of types and more upon the analysis of variation among populations.

Clearly, a new revision, based upon analysis of a large series of specimens representative of the various geographic populations, was indicated. To such a morphological analysis, information from the life-history and ecology of the populations and the data from the palaeontological record should be added.

The present study was a natural development from a prolonged research program in the ecology and management of North American caribou (Banfield, 1949, 1954b, and 1955). A better understanding of the relationships of Nearctic populations was the first objective. With further study it became evident that the Nearctic and Palaearctic forms should be compared. Subsequently the extinct material was reviewed in the light of the differentiation of the living forms in order to produce a single synthesis. Personal association with many of the American caribou research workers gave me the opportunity to ask for a large series of new specimens from areas formerly poorly represented. During the period 1957 to 1960, most of the American museums containing large collections of caribou were visited for study. In addition, my Department gave me the opportunity to visit important museums in Northern Europe during the summer of 1959 to measure specimens.

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VERNACULAR NAMES

There has been almost as much confusion in vernacular names for the species as in scientific names. All western European names are thought to be derived from "reino," the Lapp name for a young reindeer (Dutilly, 1949). Thus we have—Scandinavian, ren; German, Rentier; English, reindeer; Old English, Rain-Deer, Rein; French, renne; Old French, rangier, rangifère. From the last form Gesner (1551) apparently produced the presently accepted generic name *Rangifer* (Linnaeus, 1746).

The early English explorers to northern Canada, such as Mackenzie, Hearne, and Franklin, generally used the familiar name "reindeer" to describe the native American animal. Since it was the only native deer on the Canadian tundra, the name was quickly shortened to 'the deer,' and until the twentieth century the animal was known by that name throughout the English fur country.

The early French explorers to eastern North America introduced two new names for the species. The first reference to caribou is probably that of Marc Lescarbot in 1609. There are many references to caribou in the *Jesuit Relations* from the same period. Other early references are Jérémie (1720) and De Charlevoix (1744). The spelling often varied from cariboo, caribous, cariboux, caribo, carriboo, to carraboe. The origin of the word is from the Miemac Indians of New Brunswick. They called the animal "Xalibu"—the pawer or shoveller, in reference to its habit of pawing through the snow in winter to reach its food (Wright, 1929). The early French Acadians undoubtedly picked the name up from the local Miemac Indians.

Much later, when the French Canadian name was adopted in English literature, errors arose as to its derivation. Richardson (1854) erroneously reported that caribou came from the French words "quarré-boeuf" (square ox), because of its antlers(?). Another suggestion was that it was derived from the French words "carré boeuf" (four-horned ox), which seems a little more appropriate. However, the Miemac Indian name is undoubtedly the source of the present name.

Early French authors (i.e. De Charlevoix) also referred to the animal as the "asne sauvage"—wild ass. This was probably the descriptive name first applied by the French immigrants because of the animal's blunt muzzle and perhaps because of its lack of wariness. That name, fortunately, lost out in favour to the local Indian name "caribou."

Since there is only one species involved, caribou and reindeer are used generally interchangeably in this report. The term "woodland caribou" is

restricted to references to the forest form found in the wooded northeast North America. The term "reindeer" is applied more generally to tundra reindeer of Eurasia and northern North America. It is unlikely that the name "caribou" would be accepted for the forest reindeer of Europe and Asia even if it did have merit.

EARLY HISTORY

The early pre-Linnaean references to the species are important because often they formed the basis of early scientific names and provided important descriptions of life-history and distribution. No attempt has been made here to provide a bibliography of reindeer and caribou references. Those interested in the subject are referred to Sokolov (1933 and 1959, pp. 265-8) and to Dutilly (1949).

Some of the more important early references to the American races are reviewed below. The first reference to an American reindeer was probably that of John Cabot in 1497 who wrote of "Stagges farre greater than ours" on the newly discovered island of Newfoundland (Purchas, 1617). *Rangifer tarandus* was the only native species of Cervidae on the Island. When Martin Frobisher discovered the bay named after him in Baffin Island in 1576, it was written: "Hauing entred three-score Leagues, hee went on shore, and was encountered with mighty Deer, which ran at him, with danger of his life" (Purchas, 1617). This is probably the first reference to the American tundra reindeer. The first mention of reindeer on Greenland may have been that of James Hall in 1605 (Purchas, 1617). More detailed reports on the life-history of the species in the New World followed in the eighteenth century.

An important early reference to the habits of American reindeer was that of Jérémie (1720) for the area surrounding York Factory (Fort Bourbon) on Hudson Bay. Dobbs (1744, pp. 20, 22) translated Jérémie's observations "betwixt these two rivers (Churchill and Nelson) but a great number of the deer called cariboux which being drove from the woods by a great number of mosketoes or midges, come to the shore to refresh themselves, they are in herds of 10,000 to-gether, and spread through the country 40 or 50 Leagues in extent.

"In March and April they come from the North to the South, and extend then along the River 60 Leagues; they go again northward in July and August; the roads they make in the snow are well padded and cross each other as often as the streets in Paris. The natives make hedges with branches of trees and leave openings in which they fix snares and thus take numbers of them."

The same year De Charlevoix (1744, p. 191) described the caribou found in New France as a little shorter than the moose and in figure more like the ass or mule. He reported that it was not common in the more travelled areas of Canada. He recognized that it differed little from the reindeer.

Edwards (1743) illustrated the Greenland reindeer which he called *Capra groenlandica* (see Plate II).

Josselyn (1672) provided an early reference to caribou in New England (*vide* Seton, 1927, p. 57). Pennant (1784) gave an early general account of



Edward's (1743) plate of the Greenland reindeer

the species but unfortunately used English non-Linnaean nomenclature. Important early life-history observations were recorded by Hearne (1795). Harmon (1904), writing in 1800 of his travels in the Rocky Mountains, distinguished between two kinds of caribou: one large and dark, the other smaller and lighter. The standard work on the life-history of American caribou for many years was Richardson (1829) to be followed by Preble (1908).

PREVIOUS REVISIONS

Although 55 species and subspecies of reindeer have been described since Linnaeus's Tenth edition of *Systema Natura* (1758), there have been few summaries of the group. Murray (1866) was the first author to discuss the distribution of reindeer in time and space, although he had little information at his disposal. He concluded that reindeer came into existence in Asia during the glacial epoch and that the Siberian variety was the primitive form (p. 157). Previously he had stated that the Scandinavian variety was nearest the fossil variety (p. 152). In any event he concluded that the fossil reindeer of Europe were the same species (*Tarandus rangifer*) as the living varieties and that the Lapland form had migrated westward from Asia after the Ice Age. He recognized two varieties in North America (barren-ground and woodland) which had migrated across the Bering Strait landbridge. Greenland had been colonized from North America via Ellesmere Island, and eventually reindeer had reached Spitsbergen from Greenland. He believed all these varieties had developed from one stock, modified by the local environment (p. 152). Murray is generally credited with naming two forms—*sibiricus* and *spitzbergensis*, but it is not clear that he intended to do so.

The first important revision of the group was made by Lydekker (1898). By that time the name of the species had been reversed to *Rangifer tarandus*, and he recognized the following geographic races: *typicus* nom. nov., Scandinavian reindeer; *spetsbergensis* (Andersén), Spitsbergen; *caribou* (Gmelin), woodland caribou of North America; *terrae-novae* Bangs, Newfoundland; *groenlandicus* (Gmelin), Greenland; and *arcticus* (Richardson), barren-ground of North America.

About the same time, Trouessart (1898–1899) listed the following species and subspecies in his catalogue: *Rangifer martialis*, Pleistocene of Europe; *tarandus*, Recent of Europe; varieties: *sibiricus* Murray, Siberia; *spitzbergensis* (Murray), Spitsbergen; *groenlandicus* (Kerr), Greenland; *arcticus* (Richardson), barren-ground; *caribou* (Kerr), North America; *terraenovae* Bangs, Newfoundland.

Grant (1902) divided the reindeer into two series and listed 11 species under the main groups of barren-ground and woodland caribou. This elevation of the forms to the species level was to become the traditional American viewpoint for almost sixty years. Under the barren-ground caribou group, he listed *Rangifer tarandus*, Lapland; *spitzbergensis*, Spitsbergen; *groenlandicus*, Greenland; *pearyi*, Ellesmere Island; *arcticus*, North America and Arctic Islands; *granti*, Alaskan Peninsula; *stonei*, Cook Inlet, Alaska. Under the woodland caribou group, he listed, *terraenovae*, Newfoundland; *montanus*, Rocky Mountains; *caribou*, Maine to Manitoba; *osborni*, Cassiar Mountains of British Columbia.

Lydekker (1915) brought his previous classification up to date by the inclusion of many forms described near the turn of the century. He, too, recognized the two groupings: woodland, which he distinguished by palmate antlers without a tineless beam interval; and barren-ground group, which he distinguished by long antlers with a long tineless interval on the beam. He reasserted the belief that all named forms belonged to the single species *Rangifer tarandus*. The European forms—*platyrhynchus* (Vrolik), Spitsbergen; *tarandus* (Linnaeus), and *fennicus* Lonnberg—he did not assign to either group. The Asiatic and American forms he divided as follows: (A) Woodland Group: *sibiricus* (Schreber), *pearsoni* Lydekker, Novaya Zemlya; *caribou* (Gmelin), *phylarchus* Hollister, Kamchatka; *sylvestris* (Richardson), Hudson Bay shores; *terraenovae* Bangs, *montanus* Seton-Thompson, *dawsoni* Seton-Thompson, Queen Charlotte Islands; *stonei* Allen, *fortidens* Hollister, Rocky Mountains of Alberta; *osborni* Allen, *granti* Allen, *excelsifrons* Hollister, Point Barrow, Alaska. (B) Barren-ground Group: *arcticus* (Richardson), *groenlandicus* (Gmelin), and *pearyi* Allen. He noted that some of those races were intermediates between the two groups.

The same year the British hunter-naturalist Millais (1915) proposed a new analysis of the reindeer and caribou of the world based upon his wide hunting experiences with the animal. He wrote (p. 255), "The conclusion I have reached is that there is no basis whatever of reason for dividing the so-called woodland and barren-ground races.

"The more we study these interesting animals and learn their ranges and erratic migrations the more do we find that all, or nearly all, overlap and interbreed. I have found that *Tarandus rangifer caribou* of the Central Canadian Forests merge into their finest type and become almost a distinct subspecies in Central Labrador . . . where the animal grows as large and develops as fine horns as those of *Tarandus rangifer osborni* of the Cassiar and the Yukon."

Millais recognized Billberg's name *Tarandus rangifer* for the species, and the following subspecies: *caribou* (Gmelin), *keewatinensis* nom. nov., Keewatin District; *terraenovae* (Bangs), *labradorensis* nom. nov., Labrador and Ungava; *arcticus* (Richardson), *ogilvyensis* nom. nov., Ogilvy Mountains, Yukon; *granti* (Allen), *stonei* (Allen), *osborni* (Allen), *montanus* (Seton), *dawsoni* (Seton), *lenensis* nom. nov., Taimur Peninsula, USSR; *chukchensis* nom. nov., Kolemsh to Bering Strait; *asiaticus* (?), Siberia; *buskensis* nom. nov., Syansk and Busk Mountains in southern Siberia; *yakutskensis* nom. nov., Yakutsk and Amur regions, USSR; *phylarchus* Hollister, Kamchatka and Okhotsk coast, USSR.

Seton (1927) in his monograph on North American game tried to restore some order to the rapidly expanding list of named American varieties. He recognized four species—woodland, barren-ground, mountain, and Queen Charlotte Island caribou—and assigned 12 other named races to those species, as follows:

Species *Rangifer caribou* (Gmelin) 1788, woodland caribou
sylvestris (Richardson) 1829
terraenovae (Bangs) 1896
Rangifer arcticus (Richardson) 1829, barren-ground caribou
groenlandicus (Gmelin) 1877

stonei Allen 1901
pearyi Allen 1902
granti Allen 1902
excelsifrons Hollister 1912
caboti G. M. Allen 1914
ogilvyensis Millais 1915

Rangifer montanus Seton 1899, mountain caribou
osborni Allen 1902
fortidens Hollister 1912
mcquierei Figgins 1919

Rangifer dawsoni Seton 1900. Queen Charlotte Island caribou

Jacobi's (1931) monograph has been almost universally followed since its publication. Jacobi reaffirmed the two main series of reindeer (Superspecies or Artenkreis): A. Type CYLINDRICORNIS—tundra reindeer, and B. Type COMPRESSICORNIS—forest reindeer. He divided the tundra reindeer into two polytypic (Artengruppen) species, *tarandus* and *arcticus*, and three monotypic species, *platyrhynchus*, *caboti*, and *pearyi*. The forest reindeer comprised one polytypic species, *caribou*, and two monotypic species, *fennicus* and *phylarchus*. *Arcticus* was distinguished from *tarandus* by the possession of the American "bow" in the beam above the posterior tine, instead of the typical sharp bend of *tarandus*. I have modernized Jacobi's supraspecies nomenclature for clarity in Table 1.

Table 1. The Classification of Reindeer after Jacobi (1931)

Genus <i>Rangifer</i> H. Smith 1827	
Series CYLINDRICORNIS Jacobi 1931	
Polytypic species 1. <i>tarandus</i> (Linnaeus 1758)	
Subspecies (a) <i>tarandus</i> (Linnaeus) 1758	
(b) <i>groenlandicus</i> (Gmelin) 1788	
Monotypic species 2. <i>platyrhynchus</i> (Vrolik) 1829	
Polytypic species 3. <i>arcticus</i> (Richardson) 1829	
Subspecies (a) <i>arcticus</i> (Richardson) 1829	
(b) <i>excelsifrons</i> Hollister 1912	
(c) <i>asiaticus</i> Jacobi 1931	
(d) <i>stonei</i> Allen 1901	
(e) <i>osborni</i> Allen 1902	
(f) <i>montanus</i> Seton 1899	
(g) <i>fortidens</i> Hollister 1912	
(h) <i>dawsoni</i> Seton 1900	
(i) <i>fossilis</i> Jacobi 1931	
Monotypic species 4. <i>caboti</i> G. M. Allen 1914	
Monotypic species 5. <i>pearyi</i> Allen 1902	
Series COMPRESSICORNIS Jacobi 1931	
Polytypic species 6. <i>caribou</i> (Gmelin) 1788	
Subspecies (a) <i>caribou</i> (Gmelin) 1788	
(b) <i>sylvestris</i> (Richardson) 1829	
(c) <i>terraenovae</i> Bangs 1896	
Monotypic species 7. <i>fennicus</i> Lonnberg 1909	
Monotypic species 8. <i>phylarchus</i> Hollister 1912	

Points to be noted are: (1) *groenlandicus* was considered to be a subspecies of *tarandus* because of the prevalence of the "European bend" in its antlers; (2) *platyrhynchus* of Spitsbergen was associated with the polytypic *tarandus*; (3) Siberian *asiaticus* and the fossil reindeer of Europe, *fossilis*, were associated with polytypic *arcticus*, the tundra reindeer of the New World, because of the prevalence of the "American bow" in the antlers; (4) the identification of American mountain caribou, *osborni*, *montanus*, *fortidens*, *stonei*, and *dawsoni*—as subspecies of the barren-ground caribou *arcticus*. Seton (1927) had perhaps led the way in assigning *stonei* to *arcticus*. Jacobi also followed Seton in his arrangement of *caribou*.

In order to explain the extinction of the prehistoric *arcticus fossilis* in Europe and its replacement with the extant *tarandus*, Jacobi adopted the Continental Drift theory of Wegener (1915). He speculated that Europe and North America were connected during the Ice Age and inhabited by a single species of reindeer, *arcticus*. As the climate ameliorated, the reindeer migrated northward following the edge of the glacier as far as Narke Sound across central Sweden. However, the forest belt followed so quickly that the tundra reindeer were trapped there without a suitable habitat and extirpated. Soon after, the large glacial lakes from the White Sea to the Caspian Sea dried up, and *tarandus* was able to immigrate to northern Europe, to Spitsbergen, and eventually to Greenland, which, although already retreating from Europe, was still within reach of reindeer across the ice.

Previous authors had been hampered by a lack of information on the distribution of wild reindeer in the Soviet Union. Millais (1915) and Jacobi (1931) had not taken into consideration the morphological differences between domestic reindeer and native reindeer. Flerov (1932 and 1933) followed Jacobi with a different analysis, based upon Soviet Union material at the Leningrad Institute of Zoology. He recognized only the Linnaean species *tarandus* with the following geographic subspecies in the Old World: *tarandus*; *pearsoni* Lydekker 1902, Novaya Zemlya; *sibiricus* Murray; *valentinae* nom. nov., Siberian woodland caribou; *phylarchus*; *setoni* nom. nov., Sakhalin Island; *angustirostris* nom. nov., Bargusin Mountains; and *platyrhynchus*. Unfortunately, Flerov seemed to be unaware of Millais (1915) names for some of the Siberian races.

The Canadian mammalian taxonomist R. M. Anderson had a wide field experience with native caribou. In discussions, he held conservative views on caribou taxonomy, but in his publications he generally followed the most recent revision. In Hadwen (1932) he wrote, "I do not think there are more than three tenable species—*R. arcticus*, *R. caribou*, and *R. montanus*—and I have my doubts about *caribou* and *montanus* being distinct species. The insular Greenland and Newfoundland forms *R. groenlandicus* and *R. terrae-novae* are perhaps better retained as full species." In the latter view he undoubtedly followed the classical concept that insular forms deserved specific rank. In his paper on the status of big game mammals in Canada (Anderson, 1938), his classification followed Seton (1927) and Murie (1935). The *Rangifer* taxonomy in his catalogue of Canadian mammals (Anderson 1946) followed Jacobi (1931).

Murie (1935) reviewed the status of caribou in Alaska and Yukon Territory. He examined a number of specimens in United States' museums as a basis for his taxonomic conclusions. In general agreement with Jacobi

(1931), he concluded that the caribou under study were all subspecies of *arcticus* (Richardson, 1829) and listed *stonei*, *granti*, and *osborni* from the Alaska-Yukon region. He also mentioned *arcticus* of the Mackenzie District and *caboti* of Labrador.

In the Palaearctic Region, Flerov's (1932 and 1933) work was closely followed by another Russian author, Sokolov (1937). That author again pointed out that Jacobi had failed to differentiate between wild and domestic reindeer. Sokolov based his analysis primarily upon skull measurements. He considered that the antlers were too variable to be considered as a racial character. He recognized the following geographical subspecies in the Old World: *tarandus*, tundra reindeer of Europe and Asia; *pearsoni*, Novaya Zemlya; *valentinae*, forest zone of Asia; *phylarchus*, Kamchatka and Okhotsk Sea coast. He gave full specific rank to *Rangifer platyrhynchus* of Spitsbergen.

Ellerman and Morrison-Scott (1951) listed the following geographic races of reindeer in their check list of Palaearctic mammals, following the views of Flerov (1933): *tarandus*, *platyrhynchus*, *sibiricus*, *pearsoni*, *phylarchus*, *angustirostris*, *valentinae*, and *setoni*. They made no reference to the previous work of Sokolov (1937). They included the Arctic regions of North America and Greenland in the range of the Palaearctic species of reindeer *tarandus*.

Flerov (1952) brought his 1933 revision of Palaearctic reindeer up to date. He confirmed the existence of a single species in the Holarctic Region and listed the following Old World subspecies: *tarandus*, *pearsoni*, *sibiricus*, *valentinae*, *phylarchus*, *angustirostris*, and *platyrhynchus*. He reduced his *setoni* from Sakhalin Island to synonymy under *phylarchus*. He stated that the taxonomy of American reindeer was in a chaotic condition because of the lack of understanding of individual variation and strict comparison of pelages. He listed the following New World subspecies: *caribou*, *pearyi*, *groenlandicus*, *caboti*, *arcticus*, *terraenovae*, *montanus*, and *dawsoni*.

Similarly, Sokolov (1959) reiterated his 1937 conclusions that *platyrhynchus* deserved full specific rank and that there were only four Palaearctic subspecies of *tarandus* (i.e. *tarandus*, *pearsoni*, *valentinae*, and *phylarchus*). It would appear that these two important Soviet specialists in ungulate taxonomy have not been able to compromise their views on reindeer taxonomy over the years.

To complete the record, mention should be made of Hall and Kelson (1959). They follow Lydekker (1898) in arranging the New World forms as subspecies of *Rangifer tarandus* and list most of the named forms, as follows: *arcticus*, *caboti*, *caribou*, *dawsoni*, *eogroenlandicus*, *fortidens*, *granti*, *grönlandicus*, *montanus*, *osborni*, *pearyi*, *stonei*, *sylvestris*, and *terraenovae*. The boundaries drawn between these various geographic subspecies on map 494, p. 1019, seem incredible in some cases.

PRESENT INVESTIGATION

MATERIALS

For the many reasons described under "Individual Variation" and "Previous Revisions," the present revision is based primarily upon the comparison of adult reindeer skulls from all parts of the species range. Most institutions known to contain large collections of reindeer or holotypes were visited, and their collections of skulls were measured. A total of 855 skulls

of the nine recognized extant subspecies of reindeer were studied. The localities represented by specimens examined are listed under each subspecies. Not all specimens observed or measured were treated in the measurement summaries. Only adults, approximately four years of age or older, are listed in the appended specimen lists. Many of the skulls examined were photographed for the record.

In addition, 60 hides were examined and colour-coded, and measurements were taken of hooves and glands; many were photographed in colour. Finally, many field measurements were taken from labels and the literature.

A total of 14 holotypes of named varieties were examined. Of all the known types only the type of *Rangifer mcquirei* Figgins 1919 was not studied.

A total of 92 specimens of extinct ancient reindeer were studied in order to present vertical as well as horizontal classification of the genus *Rangifer*.

Earlier revisions were hampered by the lack of series of specimens which would have illustrated variation and of specimens from large areas of the species range in Canada.

Approximately 350 new specimens, which have been deposited in the National Museum of Canada, were obtained from various sources, particularly through the activities of the Canadian Wildlife Service. Some large series of specimens of a single sex from one population were obtained in order to appraise local individual variation. These include 12 females and 11 males from Baffin Island, 35 females and 11 males from the central of tundra Mackenzie District, 23 males and 8 females from Banks Island, 25 males from Bathurst Island, 15 males from Pelly Bay, as well as many smaller but significant series from Alaska to Newfoundland and from Ellesmere Island.

METHODS

This revision is based primarily upon adult skull measurements. I measured practically all the specimens here reported, with the exception of a few important specimens which I was not able to study. In such cases, the comparable measurements were taken from the literature. Such specimens are designated in the appendices. The larger measurements were made with arc calipers and read on a steel metric rule to the nearest millimetre. Shorter measurements such as tooth rows were made by means of a vernier caliper and recorded to the nearest tenth of a millimetre.

Standard external measurements such as total length (including tail), tail, hind foot, shoulder height, and the weight are those of the collector. In addition, certain measurements on the skins, involving the hooves and tarsal glands, were made by the author.

The greatest length of adult metacarpal and metatarsal bones was measured in a number of cases.

Capitalized colour names for pelages are from Ridgway (1912).

The cranial measurements used are illustrated in Figure 1 and defined below. The first seven measurements were used throughout the analyses. A number of others were made and used for the primary analyses and special cases such as the description of certain characteristics because of sexual and age differences, and the comparison with palaeontological specimens.

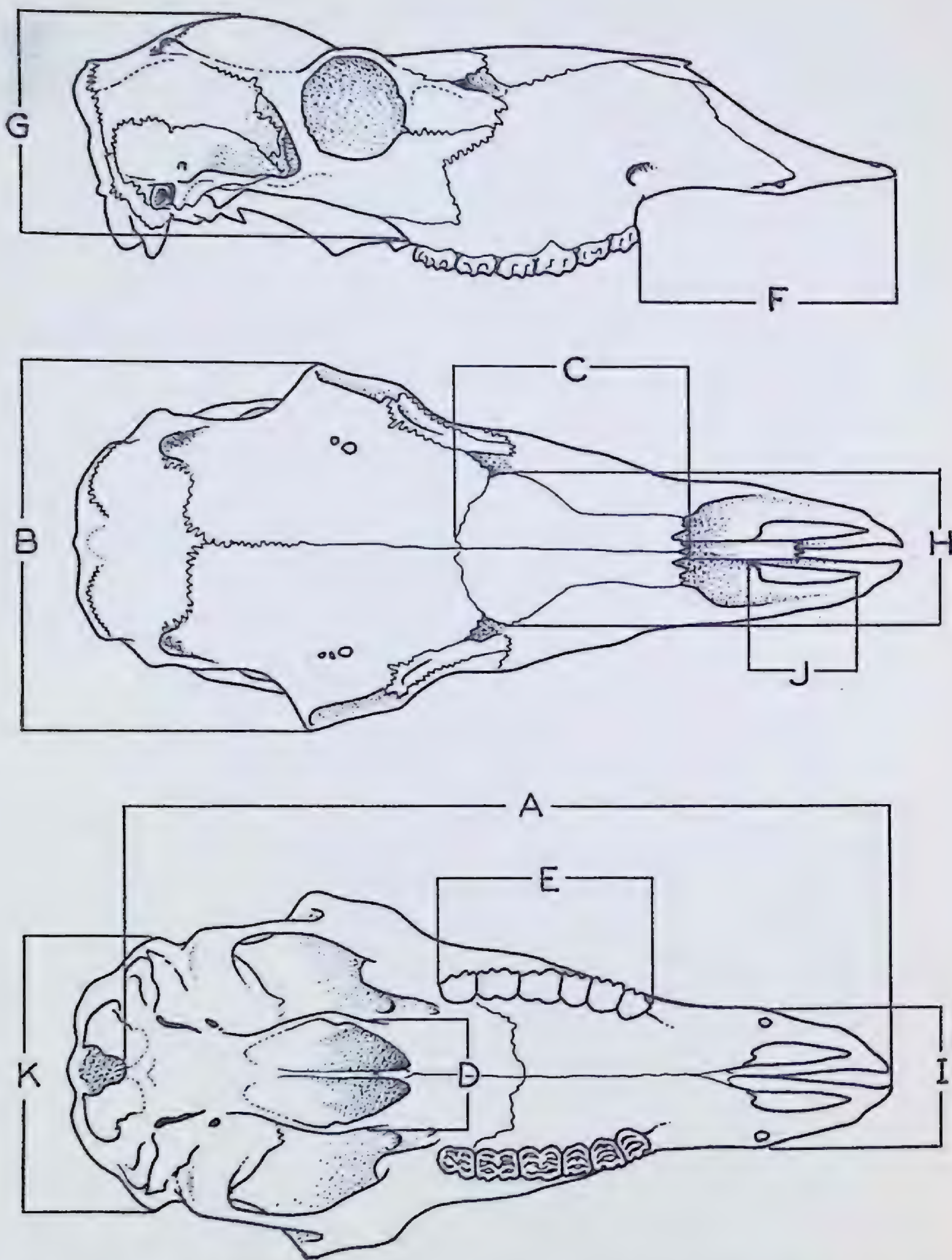


FIGURE 1. Cranial measurements taken in this investigation: A—basal length, B—orbital width, C—nasal length, D—post nares, E—tooth row, F—diastema, G—occipital height, H—nasal width, I—canine width, J—incisive foramen.

Primary Measurements

Basal length. The distance between the mid point of the inferior lip of the foramen magnum (basion) to the anterior tip of the left premaxilla (gnathion cf. Thomas, 1905).

Orbital width. The greatest distance between the lateral posterior edges of the orbits.

Nasal length. The greatest median length of the left nasal bone.

Post nares. The least outside width of the post nares openings of the palatine bones.

Tooth row. The greatest length of left maxillary tooth row, P2 to M3 at the stained gum line.

Diastema. The distance between the anterior tip of the left premaxilla (gnathion) to the gum line of the left maxillary P2.

Occipital height. The shortest distance between the posterior median edge of the palate (palation cf. Thomas, 1905) to the median point of the frontal-parietal suture.

Secondary Measurements

Nasal width. The greatest combined width of the two nasal bones.

Canine width. The combined width of the two maxillary bones at the canines.

Rostral height. The shortest distance between the palation and the mid point of the frontal-nasal suture.

Incisive foramen. The greatest length of the left incisive foramen.

Zygomatic width. The greatest outside distance between the zygomatic arches at the jugal-squamosal suture.

Mastoid width. The greatest outside distance between the mastoid processes.

Mandibular length. The greatest distance from the anterior tip to the posterior angle of the ramus.

Mandibular height. The greatest distance from the condyle to the posterior angle of the ramus.

Mandibular tooth row. The greatest length of the mandibular tooth row, P2 to M3 along the gum line.

Mandibular diastema. The distance between the posterior rim of the alveolus of I1 and the anterior side of P2 at the gum line.

Antler length. The greatest outside length of the longest antler beam from below the burr to the tip of the main terminal tine.

Antler spread. The greatest outside distance between the paired antler beams.

Beam horizontal diameter. The diameter of the beam above the bez tine in a horizontal plane.

Beam vertical diameter. The diameter of the beam above the bez tine in a vertical plane.

Qualitative Characters

Nasal type. If the anterior portions of the nasal bones rose pronouncedly above the maxillary in lateral view, the nasals were referred to as arched. If the nasals scarcely appeared above the anterior portion of the maxillary bones, they were referred to as flat.

Antler type. If the brow, bez, and terminal tines were generally broadly flattened with terminal nubbins and the beam was somewhat flattened, the antlers were referred to as palmate. If the bez and terminal tines were generally composed of long, individual points and the beams were somewhat round in cross-section, the antlers were referred to as digitate.

Foot Measurements

Hoof length. The greatest outside length of the hoof of the left fore digit number 4; from the heel of the frog (pad) to the anterior tip of the hoof.

Hoof width. The greatest outside width of the two hoofs, left fore digits 3 and 4, with the frogs and hoof tips touching each other in a pseudo-natural position.

The sexes have been grouped separately. Only adults have been used in the comparisons of measurements; i.e. skulls showing all the permanent teeth fully erupted and some significant wear on the posterior accessory cusp of the lower third molar. It has been estimated that such animals are approximately $3\frac{1}{2}$ years old (Banfield, 1954b). Only metapodials with fused epiphyses have been measured.

The comparison of coat colour has been between specimens in fresh autumn pelage, generally September. In some cases other pelages such as winter and spring have been described.

Specimens of similar sex and age were originally grouped with others known to come from the same interbreeding populations, or from contiguous geographical areas, which are not separated by geographical barriers. With the North American material, personal familiarity with most of the Canadian caribou habitat allowed me to establish reasonable geographic population groups. Literature on Alaskan caribou research by such men as Scott, Chatelain, and Elkins (1950) suggested Alaskan grouping. Degerbøl (1957) suggested Greenland grouping. The Eurasian material was grouped according to named subspecies after Flerov (1933), because there were fewer specimens to treat.

Initially the following 43 geographic groups were compared: NORTH AMERICA: (1) Maritime Provinces, Maine, and the Gaspé Peninsula of Quebec, (2) central Quebec, north of the St. Lawrence River, (3) western Ontario and Minnesota, (4) Newfoundland, (5) Labrador and northern Quebec, (6) northwestern Ungava Peninsula, Quebec, (7) Prairie Provinces and upper Mackenzie Valley, N.W.T., (8) Rocky Mountains in Alberta and British Columbia, (9) Selkirk Mountains in British Columbia and northwestern States, (10) northwest British Columbia and adjacent Yukon Territory, (11) central Yukon, (12) southeastern Yukon and southwestern Mackenzie District, N.W.T., (13) southwestern Yukon and southeastern Alaska, (14) Alaska Peninsula and adjacent islands, (15) Kenai Peninsula, Alaska, (16) central Alaska range, Alaska, (17) Steese Highway herd including west central Yukon, (18) Brooks Range, Alaska, (19) northern Yukon,

(20) central Mackenzie District and northern Saskatchewan, (21) Dolphin and Union Straits, (22) southern Keewatin District and northern Manitoba, (23) northern Keewatin District, (24) Baffin Island, (25) Southampton Island, (26) Ellesmere Island, (27) Prince Patrick and western Queen Elizabeth Islands, (28) Banks Island, (29) Prince of Wales Island, (30) southwest Greenland, (31) northwest Greenland, (32) northeast Greenland, (33) Queen Charlotte Island, B.C. EURASIA: (34) Spitsbergen; (35) northern Scandinavia, *tarandus*; (36) Finland and northwestern Sweden, *fennicus*; (37) central USSR, *valentinae*; (38) northern USSR, *sibiricus*; (39) Trans Baikal region, USSR, *angustirostris*; (40) Western Siberia, Kamchatka; (41) Sakhalin; (42) domestic reindeer, Mackenzie Delta; (43) domestic reindeer, Labrador.

The comparable measurements of the specimens of each group were treated as population samples and analysed by standard statistical methods, which involved the calculation of mean, standard deviation, standard error of the mean and coefficient of variability. Those statistics, along with the number of specimens in each sample and range, are recorded for the groups in the appended Tables 8 to 22. The group means were compared using Duncan's (1955) Multiple Range Tests. The results of those tests are indicated in the tables by asterisks denoting the level of significance (*5 per cent, **1 per cent) attained by differences between adjacent means. Bracketed means indicate differences between means above those levels of significance.

Such tests were initially conducted on the various geographical groups. When the differences between means were found to be insignificant, the samples were amalgamated on the basis of geographical and biological association until the recognized geographic subspecies were reached. The quantitative analysis was found to be in agreement with the other data utilized.

A problem arose in the application of Duncan's tests because the number of specimens varied in the samples. The problem was met by using the harmonic mean of the sample numbers, a procedure which is adequate for comparisons involving numbers more or less alike. Where sample sizes were small, the results were checked by standard t-test procedures. Those checks supported the conclusions drawn previously with the harmonic means.

Although the use of ratios and indices is prevalent in taxonomic papers, I decided against their use in this treatment because of their doubtful validity. The use of ratios necessitates the acceptance of two assumptions: that the relationship between the two variates is a straight line and that the line passes through the point of origin. In measurements such as those used, these assumptions were difficult to accept.

In view of the limitations in the interpretation of ratios and their effect of masking the true relationship between dependent variables, coefficients of correlation between several variables (Table 22) and regression line equations (Table 23) were calculated. The results of these analyses raise some interesting points. In the first place there was no strong correlation between many variables and basal length. Maxillary tooth row is a good example. It varied independently of basal length; indeed in one case there was a negative correlation, indicating that the tooth row decreased with basal length increase. Such a situation is quite possible because there is increased tooth wear with increased age. An examination of a group of

regression lines (Figure 15) indicates that there is no significant variation in regression-line slope for the various groups studied and that such regression lines are, in general, characteristic of the whole group studied. Such a conclusion indicated that nothing would be gained by considering more than one factor at a time. A discriminant functions analysis of the most promising data confirmed this conclusion. Therefore co-variance analyses were not conducted. These analyses show further that the best quantitative analysis of the reindeer data is obtained through the analysis of individual factors.

During the preliminary stages, twelve measurements were analysed. Besides the primary seven, the nasal width, incisive foramen, rostral height, zygomatic width, and mastoid width were analysed. It was found that the latter measurements followed much the same pattern of differentiation as the primary seven but showed population differences less clearly. Some showed a high degree of variability; others indicated sexual differences.

Indeed it should be mentioned that most cranial and antler factors considered showed the same general pattern of variability. The primary seven and nasal type were chosen as the diagnostic features because they showed differentiation most clearly. Finally, it was found that other external features, such as field measurements, pelage colour, hooves, metapodials, velvet colour, and antler characteristics, were all useful corollary factors in arriving at the groups presented.

INDIVIDUAL VARIATION

With the current stress placed upon populations in the diagnosis of the lower taxa, it is necessary to appraise the amount of non-geographic variation before one can study taxonomic variation. Unfortunately, reindeer are a highly morphologically variable group. Besides the random genetic variation in the herds, other differences associated with age and growth, sex, annual cycle, pathology, and abnormalities must be taken into account. The variation found among reindeer during the current study associated with each of these factors is described below.

Growth

Considerable confusion has developed in the past by describing reindeer subspecies on the basis of an immature animal (as is the case with *Rangifer tarandus valentinae* (Flerov, 1933) or by comparing populations taxonomically on the basis of specimens of various ages. The present taxonomic study is based upon the comparison of adult specimens. However, before work was commenced, it was necessary to ascertain when the growth rate levelled off.

The determination of age of reindeer by means of the eruption and wear of teeth was developed independently by Banfield (1951b and 1954b) and Skunke (1952). This method provided a means of obtaining the approximate age of the museum specimens, but it was still necessary to establish when the growth curve levelled off. Fortunately a collection of domestic reindeer skulls of known age (ear-tagged when calves) from the government reindeer station at the Mackenzie Delta, N.W.T., was available at the National Museum of Canada. The measurements of these skulls and three other unaged adults from the same locality are presented in Tables 2 and 3.

Several important facts may be observed in these tables. In the first place, skull growth continues to approximately four years of age (particu-

larly among the males). Secondly, males are appreciably larger than females of the same age. Thirdly, individual variation in skull measurements occurs independent of age. Lastly, the tooth row measurement has a tendency to decline with increasing age.

It had previously been determined that the heel of $\overline{M3}$ was the last cusp of the dentition to receive wear at approximately three years of age (Banfield, 1954b). It was therefore arbitrarily decided to compare the measurements of only those skulls which showed the $\overline{M3}$ heel worn. That is believed to occur at the age of about four years under conditions of normal wear.

No special study of the growth of the immature skull was conducted. This facet was investigated by Sokolov (1937). He reported that the annual increase in width of the skull at the orbits is much less than the increase in skull length. The growth in the rostral part is much quicker and more prolonged than in the occipital region. The zygomatic width lags behind the growth rates in other parts of the skull. The most intensive and prolonged growth takes place in the occipital region (particularly width). The rate of growth in skull height is less than it is in length and width.

In the current study it was noted that the occiput of males became more rugose with age. It was found that the measurements of zygomatic breadth and mastoid breadth varied more with sex and age than as taxonomic indicators and were therefore dropped from further taxonomic consideration.

The normal growth of the antler pedicels with increasing age (Banfield, 1960) also affects the cranial bone sutures. At one time the frontal-parietal suture pattern was considered of taxonomic value. However, Wollebaek (1926) first pointed out that the great growth in the pedicel diameters (particularly of the bulls) crowded the parietal bone until it appeared only as a slip between the pedicels.

In the preliminary stages of the present investigation a measurement was made across the pedicels (pedicel width). As it soon became obvious that the measurement varied with age and sex rather than geographically, it was discarded.

Caribou calves are unique in the precocious development of antlers at about three months of age. These first antlers, developed by both sexes, are much later in shedding velvet and in being shed than in the adults. Each subsequent year both sexes of caribou generally develop a new set of antlers. As the animal grows in vigour, each succeeding set is larger and more elaborate. Eventually in old age the antlers decline in size and complexity. Little information is available on the approximate age of this decline for reindeer, or on the similarity of the annual sets of antlers. The whole matter of antler growth has been described elsewhere (Flerov, 1952, and Banfield, 1954b).

Sexual Differences

The sexes differ significantly in reindeer. Females weigh approximately 75 per cent as much as the males and are smaller in all measurements, as will be seen in the following tables and diagrams.

Table 2. Growth of Reindeer Skulls as Indicated by Measurements of Eight Males of Known Age

No.	Age, Years	Basal Length	Orbital Width	Orb. Foramen Width	Nasal Length	Nasal Width	Post Nares	Tooth Row	Canine Width	Incisive Foramen Length	Diastema	Rostral Height	Occipital Height
22414	2½	305	155	75.6	103	60.2	38.4	91.3	62.4	45.6	108	87.5	134
22406	3½	315	160	77.5	94.1	65.4	39.8	88.2	64.8	49.9	116	86	131
22407	3½	325	157	75.2	129	55.0	38.1	91.8	61.9	43.0	119	86	142
22411	3½	330	164	77.9	111	62.3	40.4	90.9	65.3	52.3	119	95	135
17196	4	322	164	81.4	92	52.8	38.1	89.0	64.4	45.6	113	81	131
22078	6	355	174	84.6	105	64.5	49.8	89.0	78.0	59.4	139	96	152
-	ad.	363	186	80.9	107	60.7	-	83.0	75.0	64.5	143	-	-
18155	S*	340	170	82.0	109	57.2	41.5	83.7	72.7	54.4	131	97	142

S*—senile, teeth heavily worn.

Table 3. Growth of Reindeer Skulls as Indicated by Measurements of Six Females of Known Age

No.	Age, Years	Basal Length	Orbital Width	Orb. Foramen Width	Nasal Length	Nasal Width	Post Nares	Tooth Row	Canine Width	Incisive Foramen Length	Diastema	Rostral Height	Occipital Height
4873	1½	263	130	64.1	100	51.8	31.7	89.6	46.9	43.7	92.3	78	111
22410	6	310	149	69.0	94.5	52.8	38.5	92.6	61.0	46.4	114	86	124
22412	8½	305	146	-	98.7	50.5	33.7	91.2	58.3	50.7	114	80	120
22409	9	314	157	71.7	94.3	61.6	39.5	88.3	69.1	47.5	120	85	123
22413	10½	322	161	77.0	97.5	53.1	39.5	83.3	64.2	43.8	122	89	134
17195	ad.	312	163	-	-	-	38.5	82.0	63.0	48.8	118	83	137

Besides size, there are other secondary sexual differences. The female antlers are much smaller and simpler in form than those carried by males. In most populations there are a few antlerless female reindeer, but in some populations of forest caribou in America and Asia the percentage of antlerless females may be as high as 40 per cent. Lactation and pregnancy seem to weaken antler growth and to delay velvet shedding and final dropping of the antlers.

The sexes of skulls may usually be determined by the pedicel diameter, those of the males being much larger. Pedicels of female skulls are usually of small diameter, separated by a broad segment of the parietal bone.

In adult females the occiput is less broadly developed than in the males. Viewed from the ventral side, female skulls are usually much narrower in mastoid width than in zygomatic width. In males these two measurements are more nearly equal.

Little can be said concerning pelage differences because of individual genetic variation. However, there is a tendency for the females to be lighter in colour with less pronounced dark faces, white necks, and flank stripes. Pregnancy also has a marked effect in delaying the summer moult.

Because of the significant differences in measurements between the sexes, males and females are segregated in the present study. It would be incorrect to lump the sexes together unless one were sure that the samples contained the same proportion of the sexes. Samples containing predominantly one sex would not have means comparable with other samples of different sex ratios. Of course, means may be devised to adjust one sex to measure the same as the other, as was done by Manning (1960).

Annual Cycle

The annual growth and shedding of the antlers have been described for the woodland caribou by Moisan (1956 and 1957), for the barren-ground caribou by Banfield (1954b), and for Eurasian reindeer by Flerov (1952) and Sokolov (1959).

Starting with Caton (1877), there has been some confusion concerning the number of pelage moults in a year. Caton thought that there should be two, spring and autumn, but admitted that most observers had mentioned only the one in the spring. Banfield (1954b) described only one pelage moult, in summer, and concluded that the winter colour was produced by growth of the hair, bleaching, and the loss of the dark tips by breakage. However, Sokolov (1959) reported an autumn change of coat in addition to the summer moult. He reported (op. cit, p. 270) "The lightening takes place due to the fact that beginning with the end of summer longer hairs of white colour grow through the summer hair, which is brown colour, in an ever increasing number and cover up the summer colour. The transitional grey colour of the autumn fur depends on the mixture of white and brown hairs."

The most striking effect may be observed on the neck. In early autumn this is generally grey in many populations, but by late autumn it is creamy white. A re-examination of autumn pelts in the National Museum of Canada has shown that the grey colour of early September is produced by a mixture of white-tipped guard-hairs among the clove brown hairs of the summer coat. The growth of these white guard-hairs into the long throat fringe undoubtedly covers the brown guard-hairs. This observation tends to

confirm Sokolov's analysis. However, the dirty dorsal colour of early spring is undoubtedly caused mainly by bleaching and tip breakage which exposes the dull leaden basal colour of the guard hairs.

The woolly fur which also develops in late summer under the guard-hairs is shed in the early summer with the guard-hairs. The exact time of the moult and the subsequent progress of the pelage renewal depend upon the sex, age, and physical condition of the animal.

The difference in pelage colour throughout the season is profound. The new summer coat is short and dark; the early winter coat is long and is generally characterized by contrasting light areas. The late spring coat is generally much faded to a light salt-and-pepper shade, and the light areas are not so clearly marked. The uselessness in comparing hides taken at different seasons is clearly evident. Unfortunately such comparisons have been made in the past.

In the current study, geographic subspecies are compared on the basis of fresh early autumn skins taken from late August to early October.

The annual transformation of the hooves was described by Flerov (1952) and briefly in this report under specific diagnosis.

Abnormalities Due to Pathology

A disease resembling lumpy jaw, or actinomycosis, is known to infect wild reindeer herds in Canada (Banfield, 1954b, vol. 2, p. 42). In a field study of 380 skulls of barren-ground caribou, 2.1 per cent showed lesions of necrosis of the mandibular and maxillary tooth alveoli, and bony exostosis of the mandibles. Degerbøl (1957) has reported similar lesions from Greenland. During the current study three additional specimens with actinomycotic lesions were found: USN 21343 (the type of *R. t. phylarchus* from Kamchatka, U.S.S.R.), USN 246523 from Alaska, and NMC 23439.

In specimen NMC 21850 the premaxillae bones appear to have been fractured during life.

Domestication in zoological gardens or close herding on confined ranges has a profound effect upon normal calcium metabolism. Zoological garden specimens may often be recognized by the extreme lightness of the skulls and bones. In extreme cases, as was noted in skulls of Lapland reindeer raised in Scotland, the bones become extremely thin, flaky, and fragile. All such specimens were rejected in this study.

Skull Abnormalities

Some of the skull variations found were so remarkable as to be considered abnormalities. Specimen NMC 22011 lacked the lachrymal vacuity which would seem to be an exception to the family diagnosis. In specimen NMC 22514, the nasal bones were incomplete, and the turbinate bones visible between the maxillary and nasal bones. In a number of specimens the nasal bones were distally slit (NMC 21758, LIZ 3009, and NMC 22803). In the last specimen the slits were 57 mm long, or approximately one-half the length of the bones. In specimen USN 146360, the accessory supramaxillary bone, which normally separates the premaxillary and nasal bones, was extremely long, and the premaxillary much shortened. In other examples the supramaxillary bone was absent, and the premaxillary bones almost



(Left) Asymmetrical woodland caribou skull (NMC 22073)



(Right) Mandible

touched the nasals (a cervine character). In specimen NMC 2265 the nasals were extremely narrow.

In several specimens the occipital condyles were separated ventrally by only a narrow fissure (BCGC 331 and MCZ 24890).

Three specimens indicated abnormalities in growth. In specimens NMC 2544 and NMC 25444, the rostral portions of the skulls are slightly asymmetrical with the premaxillae bending to the left. There is pronounced asymmetry in specimen NMC 22073, which starts in the occipital region near the pedicels. From that point distally, the left side of the skull grew longer than the right side so that the rostral portion is twisted to the right (see Plate III, Left).

Dentition

The normal dentition is described in the section dealing with the generic diagnosis. During the investigation a considerable number of deviations from the norm were discovered. Some of these were again important enough to be exceptions to family and generic definitions, such as the absence of a heel on the lower $\overline{M\ 3}$, or the occasional junction of the conids to adjacent lophids on $\overline{Pm\ 4}$.

Since the upper canines normally do not pierce the gums, the shedding of the deciduous canines must be a problem. The occasional retention of both pairs of canines in the alveolus is therefore not unexpected. The rare absence of the fourth pair of incisiform teeth suggests that their assignment as independent canines is correct. The occasional appearance of a $Pm\ 1$ confirms the notation of the normal $Pm\ 2 - Pm\ 4$ series. Molar teeth are occasionally absent, usually causing their opposite numbers to develop unnaturally without wear. The rotation of teeth through 90 degrees seems to be limited to the posterior tooth in the premolar and molar series—i.e. $Pm\ 4$ or $M\ 3$. The occurrence of supernumerary molars, although rare, is regular among mammals and requires no special comment here. The dental abnormalities found are listed in Table 4.

A general observation on dentitions was that in the Arctic Island form *R. t. pearyi* the maxillary molar series seemed to erupt tilted outwards and to roll into natural position. This appeared to be caused by crowding normal-sized teeth into a shortened palate.

Individual Variation

Besides these variations associated with known factors, there was a wide range of genetic individual variation that apparently was not associated with geographic distribution.

Skull. Amongst the various measurements taken, the distance between the supraorbital foramen seemed to vary without particular significance. The nasal bones seemed to be particularly variable. It was difficult to ascertain which features were taxonomically significant. The width of the nasal bones seemed to have little significance. Dr. Magnus Degerbøl of Copenhagen places considerable importance on the shape of the posterior margin of the nasal bones in distinguishing Nearctic from Palaearctic reindeer. He believes that a relatively straight transverse frontal-nasal suture is a characteristic of Palaearctic subspecies and that the Nearctic subspecies

Table 4. List of Abnormalities Found in Reindeer Dentition

Abnormality	Specimens
Incisors fused.....	AMNH 30033
Both <u>C</u> absent.....	<i>Vide</i> Banfield (1954b, 10B, p. 6).
Left <u>C</u> absent.....	NMC 2282, NMC 23431
Right <u>C</u> absent.....	NMC 22791
Both <u>C</u> absent.....	NMC 2265, CM 6794
One milk <u>C</u> with permanent <u>C</u>	NMC 2267
Both milk <u>C</u> present with permanent <u>Cs</u>	NMC 22511
Right <u>C</u> worn indicating it erupted.....	NMC 23443
<u>C</u> bifurcated.....	NMC 27836
Right <u>C</u> impacted and lying flat.....	NMC 27839
Right <u>Pm</u> 1 present.....	NMC 22783, NMC 22010
Right <u>Pm</u> 1 present.....	NMC 23438
Both <u>Pm</u> 1 present.....	MCZ 21954, USN 246523
Right <u>Pm</u> 2 absent.....	NMC 24347
Right <u>Pm</u> 2 and 3 absent.....	NMC 23445
Both <u>Pm</u> 4 lack typical independent conids...	NMC 22094, NMC 22978, NMC 22808
Both <u>Pm</u> 4 rotated 90 degrees.....	NMC 21759, LIZ 13572
M2 and M3 absent.....	AMNH 129367, <u>M2</u> and <u>M3</u> dropped
Left <u>M3</u> absent.....	USN 261164
Right <u>M3</u> absent.....	NRM D2
Right <u>M3</u> absent.....	LIZ 18324, <u>M3</u> dropped
Both <u>M3</u> absent.....	NMC 24353, <u>M3</u> did not erupt
M3 tilted.....	AMNH 30033
Right M3 rotated 90 degrees.....	NMC 14949
Both M3 rotated 90 degrees.....	NRM 702
Both M3 lack posterior heel.....	NMC 22824, NMC 22978 NRM 1894, NRM 702, BM(NH) 2536 BM(NH) 2535, BM(NH) 2531, LIZ 18324
Left supernumerary <u>M4</u>	USN 111700
Two supernumerary <u>M4</u>	USN 245612, both single cusps
Supernumerary tooth between <u>M2</u> and <u>M3</u> ...	UKM 2257, left, single cusp

exhibit a median "V" with the point directed anteriorly. After discussing the matter with him, I watched for the character among the skulls studied. Although no figures were kept, his analysis seemed to hold fairly well. The anterior tips of the nasal bones are also variable. Each nasal bone has two distal points, a median and a lateral, separated by a bay. The median points are usually the longest, but the lateral points are frequently longer.

Occasionally the median points are lacking, and the two lateral points are separated by a wide bay. The various types of nasal tips were noted in most geographic subspecies. It may be that certain types were more prevalent among certain forms. The longer median points seemed to be dominant in the tundra reindeer; the longer laterals appeared to be more prevalent in the forest reindeer; whereas nasals lacking median points were found in several specimens of Spitsbergen reindeer. However, no special study of the character was undertaken.

A number of other measurements, such as the mandibular measurements, incisive foramen length, rostral height, and canine width, seemed to have some taxonomic significance but were related to other skull measurements which showed the same features better.

Antlers. The extreme individual variation among reindeer antlers is well known. However, during the early period of reindeer taxonomy, differences in antler formation were held to be diagnostic (Gmelin, 1788). Antlers were important in the American races described by J. A. Allen. The importance of antlers probably reached its zenith in Jacobi's (1931) revision.

There can be no doubt that the basic cervid antler patterns are genetically controlled, as shown by Pocock (1933). However, recently the importance of nutritional level upon antler production has been recognized (Severinghaus, *et al.*, 1950). The fact that the mineral content of the soil and the availability of food control the size of cervid antlers is recognized by the trophy-hunting fraternity. It can be demonstrated that the finest trophies come from certain predictable geological regions. In view of the extreme variability in antlers because of sex, age, nutritional level, other physiological conditions (such as castration or pregnancy) and mineral content of the local soil, recent taxonomists such as Sokolov (1937) and Flerov (1952) have not emphasized antler formations as diagnostic characteristics of local reindeer populations. I obtained an appreciation of antler variability as a result of the study of approximately a thousand reindeer skulls during the present investigation. It was concluded that racial characteristics in reindeer antlers could be described only in the broadest terms. Observed individual variation among populations prohibited one from placing too much weight on particular antler formations.

Pelage. The same broad individual variation in pelage colour may be observed even after allowances have been made for age, sex, and season. The colour-coding of comparable skins from the same herd often indicated wide individual variation. Some impression of variation may be obtained by examining the many excellent photographs of Newfoundland caribou in Dugmore (1913)

Degerbøl and Krog (1959) have also shown that the number of roots on $\overline{\text{Pm}}\ 4$ is variable and will not separate New and Old World reindeer, as was previously postulated.

Geographical Variation

After such a recitation of individual variation, the reader might wonder if any characters were found associated with geographical distribution. A number of skull characteristics were found to be taxonomically important.

These were skull length, width of orbits, length and shape of nasals, arching of nasals (nasals rising well above maxillary bones when viewed from the side), length of rostrum, height of occiput, inflation of frontals with accompanying median well, width of post nares, relationship of maxillary tooth row to total length. These characteristics are expressed by the primary measurements listed under methods.

In addition to the skull characteristics, a number of external features were valuable taxonomic indicators. These included general form and colour of antlers, colour of antler velvet, general pelage texture patterns and colour, size as indicated by total length, hind foot, shoulder height, and weight, and finally shape and size of hooves. In addition, some aspects of the biology of the local groups have taxonomic significance.

TAXONOMIC SECTION

Family CERVIDAE Gray (1821) Deer

Diagnosis

Artiodactyls: generally cervicorn proper (males with permanent solid paired frontal bony pedicels below deciduous antlers); ulna distinct; fibula rudimentary, articulating with inferior epiphysis of the tibia; navicular and cuboid bones united; two orifices in the lacrimal bone; dentition: brachydont to subhypsodont, selenodont; no gall bladder, preorbital glands present (except *Capreolus*) two pairs of mammae, placentae polycotyledonous but with few cotyledons.

Subfamily NEOCERVINAE Crette 1922

New World Deer (including RANGIFERINIDAE Brookes, 1828, p. 61, *vide* Palmer, 1904, p. 767; RANGERINAE Gray, 1852; TELEMETACARPI (in part) Brooke, 1878; CAPRIOLINAE Pocock, 1910; RANGIFERINAE Pocock, 1923; ODOCOILEINAE, Simpson, 1945 (in part)).

Diagnosis

Telemetacarpalian (lateral metapodial bones represented by distal portions (splints) and associated cartilages, muscles and phalanges, proximal portions represented only by ridges on proximal ends of canon bones (3 and 4 metapodials)); post nares divided by a post palatine vertical plate of the vomer; premaxillae generally do not meet nasal bones; upper canines not developed for defence.

Tribe RANGIFERINI Simpson (1945)

Diagnosis

Contains only one genus *Rangifer* H. Smith, 1827. Characters as for genus.

Genus *Rangifer* H. Smith, 1827

- 1758. *Cervus* Linnaeus, Syst. Nat., 10th ed. 1: 67.
- 1827. *Rangifer* Hamilton Smith, Griffith's Cuvier Animal Kingdom, 5: 304.
- 1827. *Tarandus* Billberg, Synop. Fauna Scand. 1: 22.
- 1840. *Procervus* Blainville, C.R. Acad. Sci. Paris, 11: 392.
- 1845. *Achlis* Reichenbach, Naturges Sauget, 3: 12.

Opinion 91 of the International Commission on Zoological Nomenclature stated that *Rangifer* should be the accepted generic name and that it should date from H. Smith, 1827, with *Cervus tarandus* Linné type species, rather than from Frisch, 1775, a work that has been rejected for nomenclatorial purposes.

Type species *Rangifer tarandus* (Linné) 1758

Diagnosis

Dental Formula: $\frac{0}{3} \frac{1}{1} \frac{3}{3} \frac{3}{3} = 34$

Dentition. Subhypsodont, selenodont, rather small for size of animal, often with basal cingula and styles. Incisors small, graduated in size (I1, the largest; I3, the smallest), flexibly seated in alveoli, I1's become notched with age. Upper canines generally present in both sexes but do not pierce the gum. Permanent premolars are relatively large; the series consisting of Pm 2 to Pm 4. Deciduous lower Pm 4 with three lobes. The permanent lower Pm 4 has the metaconid as a detached column, separated from the protolophid. The entoconid and hypoconid are often similarly detached. Traces of the same independent cusps may often be seen in Pm 3 (Frick, 1937). The last lower molar M3 with a weak posterior third lobe. The posterior crest of the lower molars more or less completely isolated as is true for the anterior crescent. The posterior end of each crescent on the upper molar has a spur on it, according to Loomis (1928). He states that these are primitive characters in *Rangifer*.

Skull characteristics. Cranium moderately expanded, extreme post orbital position of the pedicels which encroach on the parietal bone, nasals prominent and expanded proximally, preorbital pit in the lachrymal bone moderate in size, lachrymal vacuity generally moderate in size. Both sexes generally carry antlers (females in some populations are antlerless), antlers large, complex, generally semipalmate, smooth with venation premaxillae prevented from reaching nasals by a small lobe of the maxillae.

Skeletal characteristics. Fourteen pairs of ribs (Frechkop, 1955), lateral digits (2 and 5) prominent, low on foot (functional) with relatively long metapodial splints, hoofs large and crescentic rather than pointed.

Soft parts. Rhinarium restricted to small oval area on upper lip (Pocock, 1923), oval tarsal gland on inside of hock; moderately sized pre-orbital gland and pedal glands on hind feet, prepuce short and abdominal as opposed to *Odocoileus*.

Antlers. These are extremely variable. Indeed one member of a pair is never the mirror image of the other. However, a general pattern is apparent in all antlers. From the burr the beam sweeps dorsally and slightly laterally over the shoulders; then it curves upward, like a bow, so that the tip generally points forward. Generally, two main anterior tines branch off close to the burr. The first one, called the brow tine, points forward over the forehead. It has a basal stalk and then generally expands into a compressed palm with several small points. The second tine—the bez—branches off the beam a short distance above the brow; however, it swings forward in a lateral arch. It, too, possesses a basal stalk and generally a compressed terminal palmation with several points. In the general region where the beam bows upward, a short posterior tine generally branches off the posterior side of the beam. It is invariably simple but may be lacking. The peak of the beam divides into a variable number of backward-facing terminal tines. These may be digitate, or the whole peak may be compressed and palmate with many short variable tines.

Considerable variety arises in the occurrence of the brow and bez tines. Generally only one brow tine is dominant, and the other develops only a simple parallel tine. However, both may be equally developed, or one or both absent. The bez tines are generally present and alike but may be quite different in structure. The antlers on females follow the same pattern but are generally much smaller than those carried by the males. They are often

simple spikes or have a simple dichotomous branching representing a short brow tine and a longer beam.

Pocock (1933) proposed a general theory of dichotomous branching to indicate homologies in deer antlers. He proposed that from a *base* above the burr the antler divides dichotomously into an anterior tine a^1 and a posterior tine p^1 . Further on, p^1 again divides into a^2 and p^2 , and so on. This allows one to give developmental notations to the various tines. Accordingly, he provides the following notations for *Rangifer* antlers to indicate homologies with other deer: brow tine a^1 , bez tine a^2 , posterior tine p^3 , and the peak a^3 ; the beam throughout its various sections is identified as base, p^1 , p^2 , and a^3 .

Reindeer antlers because of their variability do not lend themselves to the strict support of this theory. Brow and bez tines are usually characteristic enough so that they can be recognized by shape and position, even if the other is missing. When a brow tine is missing, as is often the case, the bez tine should be referred to as a^1 , according to Pocock's notation, even though it clearly is homologous with the other bez tine. Or, if the posterior tine is missing, as is sometimes the case, the upper beam would be p^3 instead of a^3 . On at least three specimens I have noted a well-developed third anterior tine (trez) which would be a^3 and would throw out all subsequent notation. Finally the terminal tines that branch off the distal portion of the beam are often very prominent and equally deserve notations p^4 , p^5 , p^6 , etc. In these cases it appears as if the anterior branch (a^3 , a^4 , a^5 , etc.) is the dominant one rather than the posterior branch.

Thus Pocock's dichotomous growth theory may be useful for many genera of deer, but its strict application to *Rangifer* does not seem so useful.

Remarks

Garrod (1877) first divided the Cervids into two groups based upon the presence or absence of the ossified vomer plate dividing the post nares. Those with divided post nares were mostly New World genera and those with undivided post nares were mostly Old World genera. Brooke (1878) followed with his division of the Cervids into the more primitive Telemetacarpi of the New World and the Plesiometacarpi of the Old World. The Telemetacarpi were characterized by retention of the distal portions of the lateral metapodials while the Plesiometacarpi possessed only rudimentary proximal vestiges of the lateral metapodials.

Although these two divisions did sort out many of the same genera, there were several genera such as *Alces*, *Capreolus*, and *Rangifer*, which did not fall into the same geographical group upon the application of each test. *Capreolus*, which seemed to be clearly an Old World form, based upon its Pleistocene and recent distribution, was a Telemetacarpal. *Capreolus* was bound to be a difficult case as it was already recognized as the only Cervid without a preorbital gland.

Brooke classified *Alces* and *Rangifer* as Holarctic forms. Both are Telemetacarpal, but *Alces* has the undivided Old World post nares while *Rangifer* has a divided post nares. Carrette (1922) required both New World characters for a genus to fit his subfamily Neocervinae. In this way *Rangifer* is included, while *Alces* and *Capreolus* revert to the Old World subfamily Cervinae.

Although this may seem to be rather an arbitrary decision, *Rangifer* possesses a number of other features which seem to place it with the New World genera. Many Old World genera possess well-developed canines, sometimes large enough to be used in defence (*Hydropotes*). Many Old World genera have the premaxillae extending to the nasal bone. In *Rangifer* the possession of tarsal glands, the deep-pocketed pedal glands on the hind feet, and the toes tied together by thin, haired integument seem to indicate a New World affinity (Pocock, 1910 and 1923). As mentioned previously, Loomis (1928) considered the dentition primitive.

It would have been convenient if the palaeontological record had also indicated a New World origin for the genus *Rangifer*, but this was not the case. The genus appeared on the stage relatively unannounced in the middle Pleistocene of Europe. The earliest record of the genus is during the Antipenultimate Glaciation phase 2 (Mindel) at Sussenborn, near Weimar, Thuringia, central Germany, approximately 440,000 years ago (Soergel, 1914, *vide* Zeuner, 1959). This was during a climatic aggradation ending with the Elster glaciation. Early specimens are rare, but by the time of the onset of the Last Glaciation (Würm), approximately 120,000 years ago, reindeer became increasingly common. In temperate North America, *Rangifer* specimens have not been reported earlier than at the height of the Wisconsin Glaciation (Flint, 1957).

Some authors, notably Mathew (1908), have maintained that the Neocervinae (Odocoileinae, Simpson, 1945; in part) was of New World origin. However, Simpson (1945, p. 268) has proposed that it is more probable that an Old World Cervine offshoot reached the New World at a relatively recent time (perhaps in the late Pliocene) and then diversified into the typical Neocervinae forms of North and South America. Because of its many primitive characters, *Rangifer* may have been near the early offshoot. The moose *Alces* was a later migrant to the New World, while the wapiti *Cervus elaphus canadensis* is a relative newcomer to North America since it is the only member of the Plesiometacarpalian Cervinae in the New World.

Rangifer has no recognized progenitors as yet. Frick (1937) postulated that *Antifer* Ameghino, 1899, from Ecuador, South America, might have an affinity to *Rangifer*. The name rests on a short piece of dichotomously branched antler which seems to show little similarity to *Rangifer* antlers in the illustration at hand. Later authors, including Simpson and Sokolov (1959), have denied any close relationship. We are therefore unable to locate the origin of *Rangifer*. We only know that it migrated into Western Europe about 400,000 years ago and later became abundant there. Its origin was probably in Alaska, Beringia, or in the mountains of northeastern Asia.

Species *Rangifer tarandus* (Linnaeus) 1758

Distribution. Late Pleistocene to Recent; Holarctic Region, Asia, Europe, Spitsbergen, Greenland, and North America.

- 1822. *Cervus guettardi* Desmarest, Mammalogie, In: Tableau encyclop. méthod. 2: 447. Late Pleistocene, Étampes, France.
- 1827. *Tarandus lapponum* Billberg, Synop. Fauna Scand., 1: 22. Recent, Scandinavia.
- 1836. *Tarandus rangifer* Ogilby, Proc. Zool. Soc. Lond.: 134. Recent, Scandinavia.

1842. *Tarandus borealis* Ruppell, Mus. Senckenbergianum, 3: 183. Recent, Scandinavia.
1852. *Cervus martialis* Gervais, Zool. Palaeo. Français Atlas, table 21, fig. 2, Pleistocene of Europe.
1879. *Rangifer muscatincensis* Leidy, Proc. Acad. Nat. Sci. Phila., 32. Late Pleistocene, Iowa, Illinois, U.S.A.
1934. *Rangifer constantini* Flerov, Jour. Mamm., 15(3): 239-240. Palaeolithic age, Siberia.
1935. *Rangifer* (?) *fricki* Schultz and Howard, Proc. Acad. Nat. Sci. Phila., 87: 273-298. Clovis Age, New Mexico, U.S.A.

Lydekker (1898) wrote: "In spite of the existence of more or less well-marked geographical races, reindeer from all parts of the northern hemisphere present such marked similarity in general appearance that it seems preferable to regard them all as belonging to a single wide-spread species of which most of the characters will be the same as those of the genus." I am in agreement with his opinion.

It is rather difficult to differentiate between species and generic characteristics. Most of the characteristics of the body extremities and pelage are clearly adaptive and therefore thought to be specific characteristics.

Diagnosis

Medium- to large-sized deer, possessing a number of physical adaptations to an arctic or subarctic environment; muzzle large, squarish, rather bovine in appearance and well furred; nostrils valvular; ears short, well furred, erect and broad, somewhat crowded behind the antlers, and not particularly mobile; tail short and well furred; hoofs black, large crescentic, well protected by tufts of fur; pelage long and dense, composed of long brittle guard-hairs and a close fine curly underfur; a long ventral mane on the throat; both adults and young unspotted (Flerov, 1952, reports that some calves have very faint spotting), colour generally clove brown above, white below; a clicking sound made in the foot when walking by sesmoid bones rubbing against other foot bones (Seton, 1909, p. 198). The hooves show a remarkable annual development. In summer the foot pads are relatively enlarged and soft; the edges of the hooves are worn quite flat so that the pad rests on the ground. In the winter the edges of the hooves grow to a remarkable length; the foot pad shrinks and becomes quite horny; the hair between the hooves becomes much longer and forms tufts which cover the pad. As a result, the animal walks on the thin crescent horny rim of its hooves, and tufts of hair cover the fleshy pad—a remarkable adaptation to winter snow conditions. Voice—hoarse grunts; socially gregarious matriarchy, polygamous, single young at birth; food mainly lichens.

RANGIFER IN THE QUATERNARY PERIOD

EUROPE

Recent summaries of ancient reindeer occurrences have been prepared by Reynolds (1933), Charlesworth (1957), Zeuner (1958 and 1959), and Degerbøl and Krog (1959). The first appearance of reindeer during the early Antipenultimate Glaciation, approximately 440,000 years ago, has been mentioned. It was absent during the temperate phases of the Last Interglacial but reappeared in increasing abundance upon the approach of the cooler tundra conditions associated with the early phases of the Last Glaciation (Würm).

It was a prominent member of the cold upper Pleistocene fauna of Europe; associated with the woolly mammoth, *Mammuthus primigenius*; hairy rhinoceros, *Tichorhinus antiquitatus*; musk-ox, *Ovibos moschatus*; cave bear, *Ursus spelaeus*; cave hyena, *Crocota spelaea*; and arctic fox, *Alopex lagopus*, from approximately 120,000 to 18,000 years ago, but survived the extinction of most of its associates at that time. Whenever warmer, boreal forest phases occurred, it withdrew northward and was replaced by the red deer *Cervus elaphus*.

Zeuner (1959, pp. 319-328) has chronicled the later appearances of reindeer in Europe:

Penultimate Glaciation, phase 2 (early), Saale, Germany, *ca.* 190,000 years ago; fauna poor but cool.

Last Glaciation (Würm) phase 1 (early), Grotte de Cotencher, Jura Mountains, Switzerland, *ca.* 120,000 years ago, forest-tundra, climate becoming colder on approach of glacier.

Last Glaciation, phase 1, Wallertheim, Germany, *ca.* 110,000 years ago.

Interstadial Last Glaciation, phases 1/2, Weimar, Thuringia, Germany, *ca.* 100,000-90,000 years ago, periglacial, temperate fauna, some steppe species and the present species indicating a cool climate.

Last Glaciation, phase 2, Thiede, near Brunswick, Germany, *ca.* 70,000 years ago, fauna loess steppe.

Last Glaciation, phase 2, Mainz, Germany, *ca.* 70,000 years ago.

Last Glaciation, phase 2 (late), Lake Constance, Switzerland, *ca.* 65,000 years ago, fauna tundra and subarctic forest.

Last Glaciation, phase 2/3, Pin Hole Cave, Derbyshire, England, *ca.* 60,000-30,000 years ago, fauna cold.

Interstadial, late, Lake Constance, Germany, *ca.* 33,000 years ago, subarctic forest, tundra, colder. The specimens were identified as *R. t. arcticus* Richardson (Canadian type) by Peters and Toepfer (1932) primarily on the so-called American bow in the antler beam. Degerbøl and Krog (1959) have discussed this character and concluded that it is a highly variable character and of doubtful use in identifying subspecies. I heartily concur in that conclusion.

Last Glaciation, phase 3, Balver Hohle, Westphalia, Germany, *ca.* 23,000 years ago, subarctic forest.

Last Glaciation, phase 3 (late), Hohler Stein, Westphalia, Germany, *ca.* 18,000 years ago, subarctic forest, reindeer but no mammoth.

Confirmation of the appearance of reindeer during the Penultimate Glaciation of Europe was given to me by Dr. A. J. Sutcliffe of the Geology Department of the British Museum (Natural History) during my 1959 visit. He has been studying a sequence of Pleistocene deposits in Tornewton Cave, Torbryan, South Devon, England. There he found *Rangifer* antler fragments in a "bear stratum" associated with wolverine and evidence of frost disturbance, under a "hyena stratum" which contained hippopotamus and red deer remains. He interprets the bear stratum as a late interstadial deposit of the Penultimate Glaciation.

Most ancient reindeer finds have been associated with human cultures. Their first appearance can be associated with the Chellean-Acheulean epoch and their reappearance with the middle Palaeolithic Mousterian culture of Neanderthal man upon the onset of the Last Glaciation. During the Last Glaciation they ranged from central Sweden, Denmark, England, Ireland, France, south to the Spanish Pyrenees in Catalonia and Altamira Cave near Santander, to Grimaldi and Monaco on the Mediterranean coast, central Italy, east to Galicia, Moravia, Trieste, Laibach, and Transylvania, the northern bank of the Danube (Charlesworth, 1957).

During the late Palaeolithic period, the reindeer record is most complete. In Aurignacian times (*ca.* 25,000 years ago) reindeer assumed a key role in the culture of Cro-Magnon Man (*Homo sapiens*). The meat was undoubtedly used for food, the skins for clothing, and the sinews for thread.

Artifacts have indicated that the bones and antlers were used for needles and tool handles. One can obtain a fair understanding of such basic use of reindeer by observing the recent utilization of reindeer products by Eskimos and Athabascan Indians in Canada. The dependence of palaeolithic man on reindeer can be appreciated by recalling the vivid artistry of the Aurignacian Cave drawings in the Dordogne, which suggested an intimate knowledge of reindeer biology. Other Aurignacian sites are at Krems and Vienna.

The importance of reindeer continued during the Solutrean period (*ca.* 15,000 years ago). Although art of that period is rare, reindeer carvings on antler and bone are known.

During Magdalenian times (*ca.* 13,000 years ago) the palaeolithic art form reached its highest achievement in colour at Altamira, Spain. It was a period when the glaciation was at its maximum and reindeer distribution at its broadest. Sculptured reindeer in the round are also known from Altamira (Charlesworth, 1957). An estimation of the importance of reindeer in the Magdalenian culture is obtained by the following analysis: at Munzingen, reindeer formed 5 per cent of the booty; at Kesslerloch, 79.4 per cent; at Schweizerbild, 75 per cent; and at Stellmoor, 100 per cent of the booty (Charlesworth, 1957).

The onset of Mesolithic times witnessed the amelioration of the climate and the northward retreat of the Last Glaciation in western Europe. Reindeer were common on the Scandinavian tundra during the Allerød period (*ca.* 12,000–9,000 years ago), but they had disappeared from central Europe during the Chancelade period (*ca.* 10,000 years ago).

Reynolds (1933) has reviewed the abundant reindeer remains in England, Scotland, and Ireland. In England they were abundant from Mousterian to Magdalenian times, after which they declined. They continued in Scotland in early prehistoric times from the Solway to the Orkneys. Remains have been found in old Pictish forts in Caithness. Their extinction in Scotland has been accredited partly to human hunting. According to the Orkneyinga Saga, they were alleged to have survived in Caithness until 1159.

There are numerous reindeer remains from Ireland, although they have not been associated with human industry. Reynolds (*loc.cit.*, p. 26) states that all the antler beams are round, and he identifies them as the tundra form. However, the illustration of the skull from Ashbourne shows rather heavy palmate antlers, suggestive of the forest type. Other antlers figured by Reynolds (*loc. cit.*, pp. 29–31) are more suggestive of the tundra forms.

Degerbøl and Krog (1959) have reviewed the Danish reindeer remains. They record over two hundred specimens. Six are referred to the Last Glacial or Late-Glacial period. Seven, including a complete skeleton, are referred to the Early Dryas (Zone 1) of the Post Glacial period. Another ten are referred to the Allerød period (Zone 2), while most of the material is referred to the Late Dryas period (Zone 3). The greater part consists

of antler fragments; there are also skeletal parts, frontlets, a nearly complete skull, and a complete skeleton from Villestoft. This unique specimen is an important key to our knowledge of ancient reindeer. I was fortunate in examining it in 1959 in Copenhagen. Degerbøl (in Degerbøl and Krog, loc. cit., pp. 49-96) has very carefully compared the Danish material with recent reindeer specimens with regard to a number of characters including skull bones, antlers, and metapodial bones. He has taken into consideration the wide variation found in living races before reaching his conclusions. Ecological and anatomical evidence indicates that the prehistoric Danish reindeer were large powerful animals inhabiting an open arctic tundra habitat. Their antlers were characterized by long cylindrical beams generally with the American bow and palmated brow. The bowed beams had previously been noted from late-glacial sites in Germany. On the other hand, recent Scandinavian *tarandus* beams usually have a sharp upward bend at the posterior tine. Degerbøl concludes that such a difference in antler form is not greater than could be expected by evolution through the approximately 12,000 years which have elapsed since the Late Dryas period. In several of the skull characteristics, the Danish ancient reindeer resembled the present Scandinavian *tarandus*. However, the teeth were generally heavier, as is characteristic with the Pleistocene specimens of other genera such as *Bison* and *Alces*. The limb bones indicated an animal of larger size than the present *tarandus*, indeed as large as the forest reindeer *fennicus* Lonnberg.

Although reindeer were the commonest large mammal in Denmark during the younger Dryas period, they disappeared at the close of that period. A single specimen is known from Holstein at the beginning of post-glacial time. They appear to have remained longer in southern Sweden. Isberg (1930) records over 150 reindeer remains in Sweden, a few of which are datable. However, 18 are thought to be post-glacial. Thirteen are thought to be of Boreal time and three at the beginning of Atlantic time.

In historical times reindeer were found in the Black Forest of Germany in Roman times, and they lingered in Poland and the Baltic States until the sixteenth century (Reynolds, 1933).

EASTERN EUROPE AND ASIA

No special efforts have been made to record reindeer finds in the Soviet Union. Sokolov (1959, p. 272) reported that ancient reindeer, dating from the beginning of the upper Pleistocene (Riss), have been found at such places as Crimea in the USSR. At the beginning of the post-glacial period, reindeer occurred in the valleys of the Dniester, Bug, Dnieper, and Donets rivers. A fragment of reindeer horn belonging to the second or third century was found in the Bug estuary.

Flerov (1934) described *Rangifer constantini* from a well-preserved skull of Solutrean age from 80 kilometres north of Irkutsk, Siberia. Reindeer remains were common in the deposit.

NORTH AMERICA

Reindeer or caribou were members of the late Pleistocene fauna of North America associated with the woolly mammoth, *Mammuthus primigenius*; mastodon, *Mammut americanus*; cave bear, *Ursus spelaeus*; various bison, *Bison occidentalis*, *B. crassicornis*, *B. alaskensis*; and various musk-oxen, *Bootherium* sp., *Symbos* sp., *Euceratherium* sp., and *Ovibus moschatus*.

Unfortunately most of the early caribou remains were reported as Pleistocene without adequate stratigraphy. They undoubtedly refer to Wisconsin times (Flint, 1957).

Hay (1923, 1924, 1927, and 1930) has summarized the various reports which are repeated here for completeness:

- Hartman's Cave, Stroudsburg, Munro Co., Pennsylvania, late Pleistocene or early Recent;
- Dumbell Harbour, Grinnell Land, Greenland 82° 30'N., late Pleistocene beds;
- Toronto, Ontario, Humber River bar, a Lake Iroquois beach of late glacial age (Coleman, 1933), associated with mammoth and muskox;
- Woodbury, Vt., antler and part of upper jaw; in bog (*R. caribou*), close of Pleistocene;
- New Haven, Conn., humerus and tibia, late Pleistocene glacial withdrawal;
- Ossining, Westchester Co., N.Y., antler in peat bog, late Pleistocene;
- Vincetown, Burlington Co., N.J., antler, Wisconsin age (*R. arcticus* ?);
- Trenton, Mercer Co., N.J., knife handle, post Pleistocene;
- Alton, Madison Co., Ill., tooth;
- Menomonee, Dunn Co., Wisc., antler, preglacial(?);
- Bigbone Lick, Boone Co., Ky., antlers;
- Lake Bonneville, Utah, bone fragments, upper Quaternary;
- Manhattan, Nye Co., Nevada, tibia and metatarsus in gravels;
- Muscatine, Muscatine Co., Iowa, bones and teeth of *Rangifer muscatinensis* Leidy (Illinoian and Iowan times?);
- Avon Polk Co., Iowa, vertebrae and right ramus, *R. muscatinensis*, Wisconsin;
- Correctionville, Woodbury Co., Wisc., antler fragments, late Pleistocene;
- Crosby, Crow Wing Co., Minnesota, antlers probably *R. caribou*, late Wisconsin;
- Alaska, Yukon, Mackenzie District, Recent and Pleistocene, *R. arcticus* (Hay, 1930) also *R. sp.*, Missouri, Pleistocene.

In more recent years, additional records of ancient reindeer have been published. Schultz and Howard (1935) described *Rangifer* (?) *fricki* in a rich faunal assemblage from Burnet Cave, Guadalupe Mountains, New Mexico. It was associated with a Clovis age point which may be dated approximately at 12,000 years ago. Frick (1937) mentioned the abundant reindeer remains from Fairbanks, Alaska. The palaeontological collection of the National Museum of Canada contains a portion of caribou antler (possibly woodland type) from Discovery Pass, Yukon Territory. Fisher and Ostrom (1952) reported a caribou antler from gravels of Lake Iroquois age, near Schenectady, N.Y. They date the period as approximately 4,500 years ago. They also report previous New York records for Scotchtown, Orange Co., Fairytown, and Sing Sing. MacNeish (1955) reported the discovery of caribou bones associated with mammoth and human industry at Great Bear River, N.W.T., approximately 5,000 years old. The caribou remains were identified as *R. pearyi*.

From these remains we may conclude that at the height of the Wisconsin glaciation perhaps 30,000–22,000 years ago, reindeer were distributed in a tundra belt across the southern edge of the ice-sheet from New Jersey, Kentucky, Missouri, Illinois, Iowa, to the mountainous region of the southwest—New Mexico and Nevada. Flint (1957) has suggested that the tundra belt was fairly narrow, because pine and spruce forests grew close to the base of the drift in Iowa and elsewhere. However, it should be remembered that reindeer often inhabit taiga regions at present. Farther west in the Cordilleran region, higher elevations and local mountain

glacials must have provided an extensive alpine tundra habitat for reindeer just as they do today in the northern Rocky Mountains.

When one recalls the Nearctic affinities of *Rangifer* and the strong indications of a boreal or arctic origin for the reindeer *R. tarandus*, one's attention quite naturally is directed to the unglaciated refugium in the Alaska-Yukon region. The loess and reworked loess of the Fairbanks, Alaska, area have been known for many years to contain rich collections of reindeer bones (Frick, 1937; Geist, 1953; and Péwé, 1958).

Dr. Troy L. Péwé of the U.S. Geological Survey, College, Alaska, has studied the stratigraphy for the Pleistocene deposits in the unglaciated Fairbanks area for the past twelve years. By means of radiocarbon dating and other parameters, he has been able to outline a local stratigraphy and to extend it to other parts of the interior Alaska with fair accuracy. Dr. Péwé (1960) in a personal communication wrote as follows:

"My interpretation of the chronology shows that we have a thick deposit of Wisconsin reworked loess which represents an age which is perhaps 70,000 years old at the base. It lies unconformably over a much older loess deposit, a deposit which at one time was frozen but perhaps was thawed during an interglacial (the Sangamon).

"All the caribou specimens that I have seen, except one, . . . come from the Wisconsin deposits. I would say that they go back at least 50,000 years . . . It is my impression that the caribou was indeed present here all through Wisconsin time and the remains are fairly abundant.

"In my unpublished material I find reference to one notation where caribou bones (identified by Geist) were collected by me from what I am interpreting to be pre-Wisconsin sediments. This would be from the Illinoian loess . . . As it is now written up in my report for the Fairbanks area, I list these specimens as Illinoian in age." (Penultimate Glaciation.)

From this valuable contribution we see that the history of *Rangifer* in North America has been pushed back to an age approximately contemporaneous with the Eurasian finds, if the glaciations were synchronous, as is generally conceded (Larsen, 1958, p. 15). Reindeer were abundant throughout the Wisconsin Glaciation in the Alaska-Yukon Refugium and probably in the Penultimate (Illinois) Glaciation as well. It is likely that they occurred in Alaska during the Last Interglacial (Sangamon) period as well, as the evidence suggests little climate change from Illinoian through Wisconsin times.

There is also one piece of evidence to suggest that they occurred in northern Greenland during the Wisconsin Glaciation (Fielden, 1877 *vide* Hay, 1923).

TAXONOMY OF QUATERNARY RANGIFER

A number of extinct reindeer species and subspecies have been described upon the basis of ancient specimens. Only Jacobi (1931) and Degerbøl and Krog (1959) have made any attempt to analyse the material. Since the last two authors did such a thorough job of comparing the Danish specimens with other European material, I have made no attempt here to duplicate their study. My own thoughts on the matter are in complete agreement with their conclusions.

The Villestofte, Funen (Early Dryas, *ca.* 12,000 years ago) specimen was measured according to my criteria in order to be comparable with the recent material. Those measurements, along with measurements of other ancient Old World reindeer, are presented in Table 5. It should be kept in mind that the specimens are not strictly comparable, because there is undoubtedly a variation of some thousands of years between the specimens. Another problem is introduced by the lack of information concerning the sex of the specimen. Although the sex of some specimens may be suspected, all comparable material must be pooled.

Degerbøl and Krog (1959) report the greatest length of six Danish subfossil metatarsi which averaged 272 mm (255–289), and seven Danish metacarpi which averaged 203 mm (199–210). I measured four metacarpi in the British Museum (Natural History) from ancient finds in England, which averaged 290 mm (282–298); and one metatarsal measured 250 mm.

Table 5. Comparison of Old World Subfossil Reindeer Skulls

	Villestofte Male	*Strangegaard Male	*Almindingen Male	**Ashbourne Male	***Irkutsk Male	Mitcham, Surrey. BM(NH) M12103	Goughs Cave, Cheddar BM(NH) M13790	Goughs Cave, Cheddar BM(NH) M13789
Antler length.....	1,270	—	—	—	—	—	—	—
Antler spread.....	1,050	—	—	—	—	—	—	—
Beam vert. diam.....	44	—	—	—	—	—	—	—
Beam horiz. diam.....	38	—	—	—	—	—	—	—
Burr width.....	128	—	—	—	—	—	—	113
Base length.....	358	360	—	—	—	—	—	—
Orbital width.....	180	—	174	—	—	—	—	—
Nasal length.....	112	117	—	131	117	—	—	—
Nasal type.....	f	—	—	—	a	—	—	—
Post nares.....	354	—	—	—	—	—	—	—
Tooth row.....	97	102	—	—	101.1	—	—	—
Diastema.....	130	—	—	—	—	—	—	—
Occipital height.....	138	—	—	—	—	—	—	—
Zygomatic breadth.....	155	150	144	—	148.5	—	—	—
Mastoid breadth.....	137	137	135	—	—	—	—	120
Mandible length.....	375	—	—	—	—	—	—	—
Mandibular tooth row.....	107	—	108	—	—	102	103	—

* from Degerbøl and Krog (1959)

** from Scharff (1918)

*** from Flerov (1934)

Reference has previously been made to the rich collection of *Rangifer* material to be found in the Wisconsin Age mucks of Alaska. The most important collection of this material is contained in the Childs Frick Laboratory of the American Museum of Natural History. I am grateful for having had the opportunity of studying this material briefly in New

York in 1959. The *Rangifer* material is very extensive. I examined 10 partial skulls, 29 mandibles, 11 metatarsi, 20 metacarpi, and 4 antlers in detail. Here, again, an age variation of at least 50,000 years makes one hesitate in grouping the specimens together as a population. However, such a step is necessary in order to compare them with recent populations. Another cautionary note is necessary because of the lack of data on the sex of the specimens. Since males are larger than females, average measurements would vary, depending upon the sex ratio of the sample.

The Alaskan ancient caribou material has been compared in Table 6 with a series of 14 (9 males, 5 females) recent skulls from the Nelchina and

Table 6. Comparison of Statistics of Alaskan Wisconsin Age *Rangifer* Skulls with Recent Alaskan Specimens

Horizon	n	Range	Mean	S.D.*	S.E.**	C.V.†
ORBITAL WIDTH						
Wisconsin.....	2	160-175	167.5	—	—	—
Recent.....	14	163-183	173.9	5.28	8.41	3.03
BURR WIDTH						
Wisconsin.....	6	108-120	118.6	—	—	—
Recent.....	6	98-115	105.5	—	—	—
ORBITAL FORAMEN						
Wisconsin.....	8	73.5-81.5	77.5	—	—	—
Recent.....	6	75.0-86.5	82.3	—	—	—
MASTOID BREADTH						
Wisconsin.....	6	124-145	138	—	—	—
Recent.....	13	105-149	122.2	14.80	4.12	12.19
ZYGOMATIC BREADTH						
Wisconsin.....	2	130-132	131	—	—	—
Recent.....	13	120-150	134.4	8.95	2.48	6.66
MAXILLARY TOOTH ROW						
Wisconsin.....	6	91.7-106.8	99.5	5.92	2.42	5.95
Recent.....	14	84.2-104.6	94.14	6.75	1.80	7.17
MANDIBULAR LENGTH						
Wisconsin.....	11	250-285	265.1	12.08	3.64	4.55
Recent.....	14	255-321	289.2	19.40	5.19	6.71
MANDIBULAR HEIGHT						
Wisconsin.....	5	120-135	125.0	7.07	3.15	5.65
Recent.....	13	125-142	133.4	7.77	2.25	5.82
MANDIBULAR TOOTH ROW						
Wisconsin.....	28	91.2-116	105.5	5.65	1.07	5.35
Recent.....	14	94.6-107	101.72	3.92	1.05	3.85
DIASTEMA						
Wisconsin.....	16	72-110	91.6	11.65	2.91	12.72
Recent.....	14	90-134	109.9	11.00	2.94	10.0

* Standard deviation
 ** Standard error
 † Coefficient of variability

Steese Highway herds of central Alaska. In view of the many variables involved, no tests of significance have been conducted. It will be observed that the statistics of the two groups are generally quite similar for the ten characters tested. There are indications that the tooth rows are longer for the ancient specimens and that the mandibular diastema is shorter as well. These characteristics are suggestive of the present-day Arctic Island subspecies *pearyi*, *cogroenlandicus*, and *platyrhynchus*. One may speculate that these ancient reindeer lived in a restricted isolated tundra environment in proximity to glaciers, conditions such as the recent Arctic Island subspecies endure at present. The current Alaskan environment seems to be more beneficial as far as the caribou are concerned.

I also measured a few of the large collection of Wisconsin Alaskan metapodials. The average length measurements of 11 metatarsi were 270 mm (243–298); 20 metacarpi averaged 192 mm (178–198) in total length. These measurements are comparable to similar measurements of ancient bones from Denmark and England, mentioned previously. Unfortunately, there are insufficient numbers of metapodials, representing the recent subspecies of reindeer, to provide a good comparison in order to indicate the size of the reindeer of glacial times. However, it seems that they were moderately large, probably larger than present-day tundra races.

The collection also contains many antlers. Most of them had round beams (only two flattened ones were seen) with palmate brow tines and digitate bez and terminal tines. There were many large antlers: three of the longest measured 1,240, 1,200, and 1,140 mm with diameters above the bez tines of 43×36 and 36×45 mm. Most antlers possessed the American bow above the posterior tine; one had a prominent European bend.

It is concluded that the caribou of Alaska in Wisconsin glaciation times belonged to the living species *Rangifer tarandus*. It would hardly be more difficult to assign them to a geographic subspecies than to assign living Alaskan caribou. The Frick Collection deserves a more intense study than I have undertaken, but in order to obtain conclusive results much more data are required on the skeletons of living caribou subspecies.

Rangifer (?) *fricki* Schultz and Howard is based upon a complete right mandible and part of the palate and right maxillary tooth row from Burnet Cave, New Mexico. The authors provide numerous measurements which may be compared to recent specimens. The most noteworthy feature of the specimen is the extremely heavy wear on the teeth leaving a cusp pattern much worn away. However, when it is compared with similar tooth rows of recent *Rangifer tarandus* showing equivalent tooth wear such as specimen NMC 9503, it is found to be similar. The metaconid and entoconid of the lower Pm 4 are joined to the adjacent lophids. However, this is the result of the heavy tooth wear which has eroded the two cusps to their bases. Similar patterns may be seen in several old specimens of recent *Rangifer tarandus*. The upper dentition is indistinguishable from many specimens of recent caribou. The Burnet Cave specimen has been compared in Table 7 with a recent male caribou specimen from the northern Rocky Mountains.

The ancient Burnet Cave mandible is similar to recent caribou specimens from the Rocky Mountains in the possession of large teeth and a long slender ramus. The describers seem to have noticed the similarity; they referred to present populations of caribou in that area. Perhaps the only

Table 7. Comparison of Measurements of *Rangifer(?) fricki* with a Specimen of *Rangifer t. caribou* from Brintnell Lake, N.W.T., Canada

	Type <i>R. fricki</i>	NMC 21850 <i>R. t. caribou</i>
Length of ramus.....	285	293
Depth of ramus at Pm 2.....	33	27
Depth of ramus at M3.....	38	39
Length of mandibular tooth row.....	105.5	111
Pm 2-Pm 4 length.....	43.5	48
M1-M2 length.....	63	63
Pm 4 transverse diam.....	13	11.5
M3 transverse diam.....	14	11.5
Mandibular diastema.....	91	105
Upper M1 length.....	17	18
Upper M1 transverse diam.....	18.5	16.5

noteworthy difference is the shorter diastema, but it is difficult to judge its significance on the basis of one comparison. I conclude that *fricki* is indeed a *Rangifer*, but that it belonged to the extant species *tarandus* and was probably a predecessor of the American woodland caribou *R. t. caribou*.

Degerbøl and Krog (1959) have concluded that reindeer specimens of comparable Mesolithic times in Denmark were probably ancestral to recent Scandinavian tundra reindeer *R. t. tarandus*. They have also pointed out that *Rangifer constantini* Flerov, of Solutrean times in Siberia, exhibited many characters of the extant Siberian forest reindeer. I agree with their conclusion that it was a primitive forest reindeer, ancestral to *R. t. fennicus*.

Other named ancient reindeer are more difficult to evaluate. *R. t. hibernicus* was probably contemporary with the reindeer *R. t. diluvii* of the Netherlands and *R. t. guettardi* of France. Comparison with present-day reindeer subspecies distribution suggests that these names are probably synonyms. However, one cannot be certain of such a conclusion without knowing the relative dates of the specimens and the rate of subspeciation. Of these names *R. t. guettardi* Desmarest, 1822, has priority.

The position of the American *R. t. muscatinensis* Leidy is unknown. As the description is fragmentary and the exact stratum unknown, it is difficult to decide whether it was an ancestral form to *R. t. caribou* and therefore perhaps synonymous with *R. t. fricki*, or perhaps ancestral to *R. t. groenlandicus*.

Based upon the information reviewed previously, the distribution of named reindeer subspecies at the close of the Last Glaciation is outlined below:

***Rangifer tarandus guettardi* (Desmarest) 1882**

1822. *Cervus guettardi* Desmarest, Mammalogie. In: Tableau encyclop. method. 2: 447.
1828. *Tarandus priscus y schottini* Sternberg, Isis (Oken), 21: 483.
1835. *Cervus priscus* Cuvier, Ossements Fossils, 4 ed., 6: 116.
1835. *Cervus destrenii, leufroyi, rebulii, tournalii* Serres, Verhandl. Holland. Maatsch. Wetensch., 22: 147.

1835. *Cervus leptocerus* Eichwald, Nova Acta Leopoldina, 17: tab. 51.
 1846. *Cervus bucklandi* Owen, Palaeont. Memoirs, p. 485, fig. 200.
 1852. *Cervus martialis* Gervais, Zool. Palaeont. Franc. Atlas, tab. 21, fig. 2.
 1909. *Cervus tarandus diluvii* Rutten, Die diluvialen Saugetiere der Niederlande, Berlin, 70.
 1918. *Rangifer tarandus hibernicus* Scharff, Proc. Roy. Irish Acad., Sect. B, 34: 63.

Type locality. Étampes, France.

Age. Palaeolithic age, 25,000–10,000 years ago.

Distribution. Europe.

Kind. Tundra reindeer.

***Rangifer tarandus constantini* Flerov, 1934**

1934. *Rangifer constantini* Flerov, Jour. Mamm. 15 (3): 239–240.

Type locality. 80 km north of Irkutsk, Siberia, USSR.

Age. Solutrean (Palaeolithic) ca. 15,000 years ago.

Distribution. Boreal forests of Asia.

Kind. Forest reindeer.

***Rangifer tarandus fricki* Schultz and Howard, 1935**

1935. *Rangifer* (?) *fricki* Schultz and Howard, Proc. Acad. Nat. Sci. Phila., 87: 273–298.

Type locality. Burnet Cave, New Mexico, U.S.A.

Age. Clovis (Palaeolithic), ca 12,000 years ago.

Distribution. Cordilleran highlands of North America.

Kind. Forest caribou.

***Rangifer tarandus muscatinensis* Leidy, 1879, (*incertae sedis*)**

1879. *Rangifer muscatinensis* Leidy, Proc. Acad. Nat. Sci. Phila. : 32.

Type locality. Muscatine, Iowa, U.S.A.

Age. Late Wisconsin, ca. 17,000 years ago.

Distribution. Periglacial tundra belt, North America.

Kind. Tundra reindeer(?).

The chronology and distribution of the various subspecies of reindeer *Rangifer tarandus* during the Quaternary Period have been outlined in Figure 2, based upon the best information at hand.

Specimens Examined

A total of 92 from the following localities: DENMARK: Villestofte, Funen, 1 (UCM). GREAT BRITAIN: Banwell Cave, Somerset, 1; Goughs Cave, Cheddar, 3; High Wycombe, 1; Brixham, 2; London, Buckingham Palace Rd., 1; Clapton, 1; Kents Cave, Torquay, Devon, 4 (BM(NH)); London, Isleworth, 1; Staines Reservoir, 1 (BM(NH)). UNITED STATES: Alaska, Kotzebue Sound, 1 (BM(NH)); Fairbanks Creek, 10; Cripple Creek, 8; UCL Creek, 1; Ester Creek, 4; Manley Hot Springs, 6; Engineer Creek, 5; Dome Creek, 1; Chicken Creek, 3; Rainbow, Seward Peninsula, 2; Livengood Creek, 1; Bear Creek, 1; Goldstream Creek, 1; Fox, Alaska, 1 (AMNH); 11 metatarsals, 20 metacarpals from above deposits, and 2 other Alaskan specimens. CANADA: Yukon Territory, Eldorado Creek, 1 (AMNH); Firth River, 5 (NMC); Old Crow, 1 (AMNH); Discovery Pass, 1 (NMC).

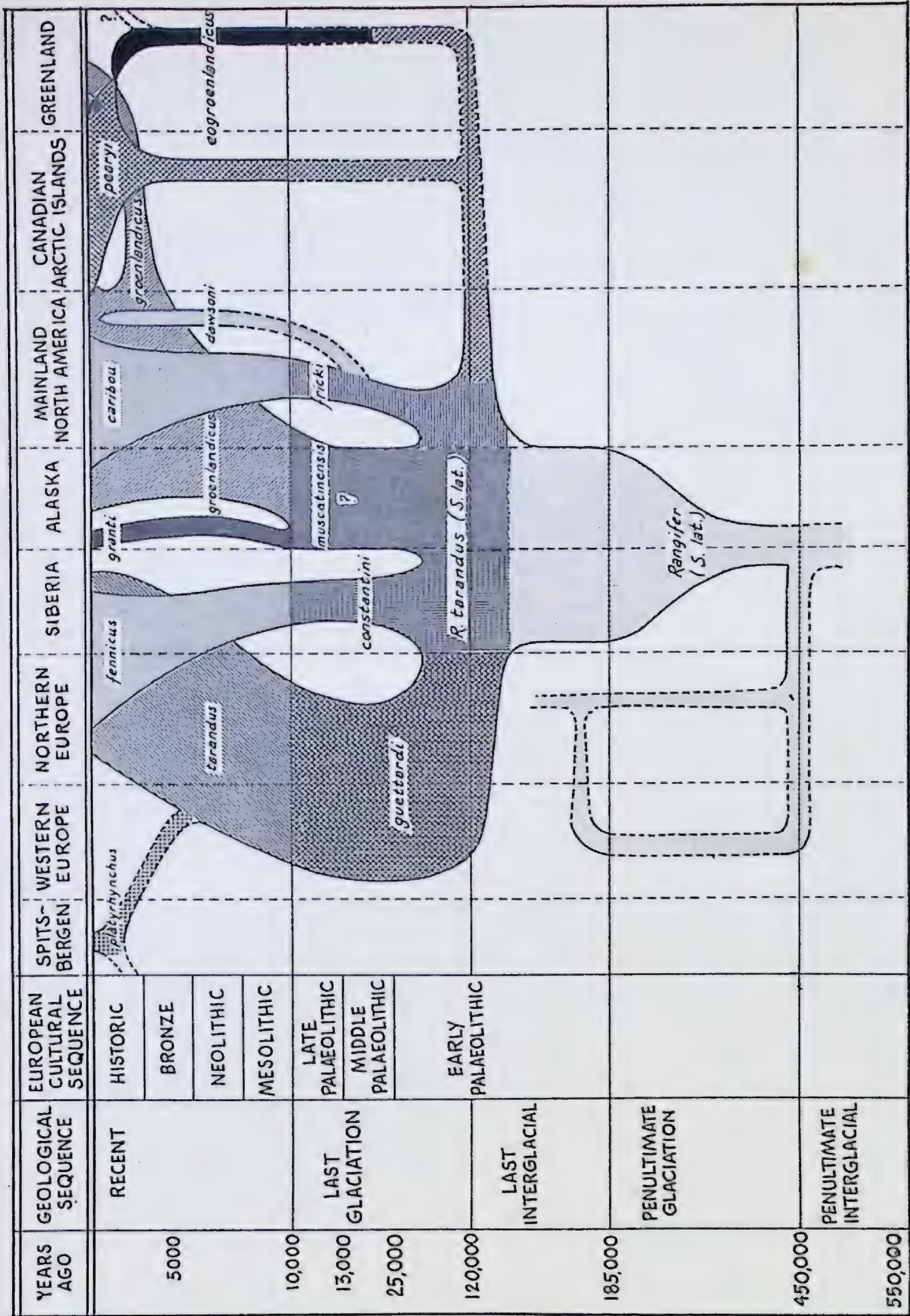


Figure 2. Chronology and distribution of reindeer *Rangifer tarandus* in the Quaternary Period. J6536.



FIGURE 3. Distribution of continental glaciations at the height of the Last Glaciation and prehistoric reindeer remains (from Flint, 1957, and the glacial map of Canada published by the Geological Association of Canada, 1958). The black circles represent localities from which specimens were examined.

DESCRIPTION OF EXTANT SUBSPECIES

GROUP CYLINDRICORNIS Jacobi 1931. TUNDRA REINDEER

Diagnosis. Antlers pale brown to ivory coloured, generally long and rangy; beams cylindrical; brow tines usually palmate; bez and terminal tines usually digitate; posterior tine usually present; well developed and farther from burr; females normally bear antlers; velvet, light brown, or sprinkled with white hairs, to pale grey; skulls short to moderate in size, rostrum foreshortened in insular subspecies, orbits protruding and angled forward, occiput more raised with inter-orbital depressions, nasals short, broad and usually flat, tooth rows shorter, without post dental ridge; body size small to moderate, legs shorter, hooves broader than long; pelage generally longer and softer than other group, clove brown; cheeks and legs paler with prominent white neck; flank stripe and belly, rump mirror, muzzle, and socks broadly white (Arctic insular populations exhibit much larger white areas); metatarsal and preorbital glands less prominent.

Of a sample of 134 *groenlandicus*, 112 possessed distally flattened nasal bones, while 22 were arched appreciably above the maxillary bones. Of a comparable sample of 132 *caribou*, 30 had flattened nasals, while 102 were arched. A χ^2 analysis indicated that such a difference in relative frequency was unlikely to occur by chance ($P < .001$). Similarly, of a sample of 52 *tarandus*, 50 possessed flattened nasals, while of a sample of 37 *fennicus*, 23 had arched nasals. Again the analysis for this character gave a significantly high value of χ^2 ($P < .001$).

Arched nasals were rarely found among the specimens of Arctic Island reindeer. It was therefore concluded that the possession of nasals flattened distally was a significant criterion for the group CYLINDRICORNIS and that arched nasals was a useful criterion for COMPRESSICORNIS.

Habitat. Tundra regions both alpine and beyond treeline in the Arctic, usually migrating to taiga in winter. Terrestrial lichens important in diet.

Biology. Gregarious, generally perform extensive seasonal migrations, to taiga; however, some populations perform only local or altitudinal migrations and do not reach forested regions in winter. Continental tundra populations perform two summer migrations (Banfield, 1954b, and Sokolov, 1959); show little wariness in herds; polygamous; mating usually occurs in herds with competition between dominant bulls and accessory bulls; dates of rut and parturition vary considerably among local populations from late September to mid-October for the rut and from mid-May to mid-June for the birth of calves; northern tundra populations in the New and Old World usually follow the later dates.

Rangifer tarandus tarandus (Linnaeus) Eurasian Tundra Reindeer

1758. *Cervus tarandus* Linnaeus, Syst. Nat., ed. 10, 1: 67.

1784. *Cervus sibiricus* Schreber, Die Säugthiere, Theil 5, Pl. 284C.

1788. *Cervus tarandus* α *rangifer* Gmelin, Linn. Syst. Nat. ed. 13, 1: 177.

1866. *Tarandus rangifer sibiricus* Murray, Geogr. Dist. Mamm. pp. 152, 155, 334. Day & Son, London (Siberia).
- 1898-99. *Rangifer t. tarandus*, *R. t. sibiricus*, Trouessart, Cat. Mamm. vivent. quam fossil., 2: 887-888.
1898. *Rangifer tarandus typicus* Lydekker, The deer of all lands: 38. Rowland Ward, London (Scandinavia).
1902. *Rangifer tarandus* var. *cilindricornis* Camerano, Mem. R. Accad. Torino, 51: 167.
1903. *Rangifer pearsoni* Lydekker, Proc. Zool. Soc. London, 1902, 2: 361 (Novaya Zemlya).
1912. *Rangifer t. tarandus* Miller, Checklist of Mamm. of Europe. 980.
1915. *Rangifer t. tarandus*, *R. t. sibiricus*, *R. t. pearsoni*, Lydekker, Cat. Ungul. Mamm. BM(NH), 4: 241, 244.
1915. *Tarandus rangifer lenensis* Millais, The gun at home and abroad, 4: 219 (Taimur Penn., Lena Delta, Kolimsk, USSR).
1915. *Tarandus rangifer asiaticus* Millais, The gun at home and abroad, 4: 222. (Ural Mts., Tobolsk, Yamal and Taimur peninsulas, upper Yenesei Mts., USSR.)
1931. *Rangifer tarandus tarandus*, *R. arcticus asiaticus* Jacobi, Das Rentier, Akad. Verslag. 64, 85. Leipzig (renaming Murray's *sibiricus*, but using a domestic type).
1933. *Rangifer t. tarandus*, *R. t. sibiricus*, *R. t. pearsoni*, Flerov, J. Mamm., 14: 331, 332, 336.
1937. *Rangifer t. tarandus*, *R. t. pearsoni*, Sokolov, Soviet Reindeer Industry, vol. 9, 100 pages.
1951. *Rangifer t. tarandus*, *R. t. sibiricus*, *R. t. pearsoni*, Ellerman and Morrison-Scott, Checklist of Palaearctic and Indian Mammals, 1758-1946, pp. 375-376.
1952. *Rangifer t. tarandus*, *R. t. sibiricus*, *R. t. pearsoni*, Flerov, Fauna of USSR, vol. 1, pt. 2, Musk deer and deer, 239-242.
1959. *Rangifer t. tarandus*, *R. t. pearsoni*, Sokolov. Fauna of USSR, 1(2) Ungulates, 279.

Holotype. None designated.

Type locality. Mountains of northwest Sweden (north Dalecarlia, Särna, Idre districts (Lonnberg, 1909).

Diagnosis. As for CYLINDRICORNIS.

Description

See Tables 8 and 9 and Figures 8 to 15 for comparison of statistics of skull measurements between this subspecies and its neighbours.

Average Skull Measurements

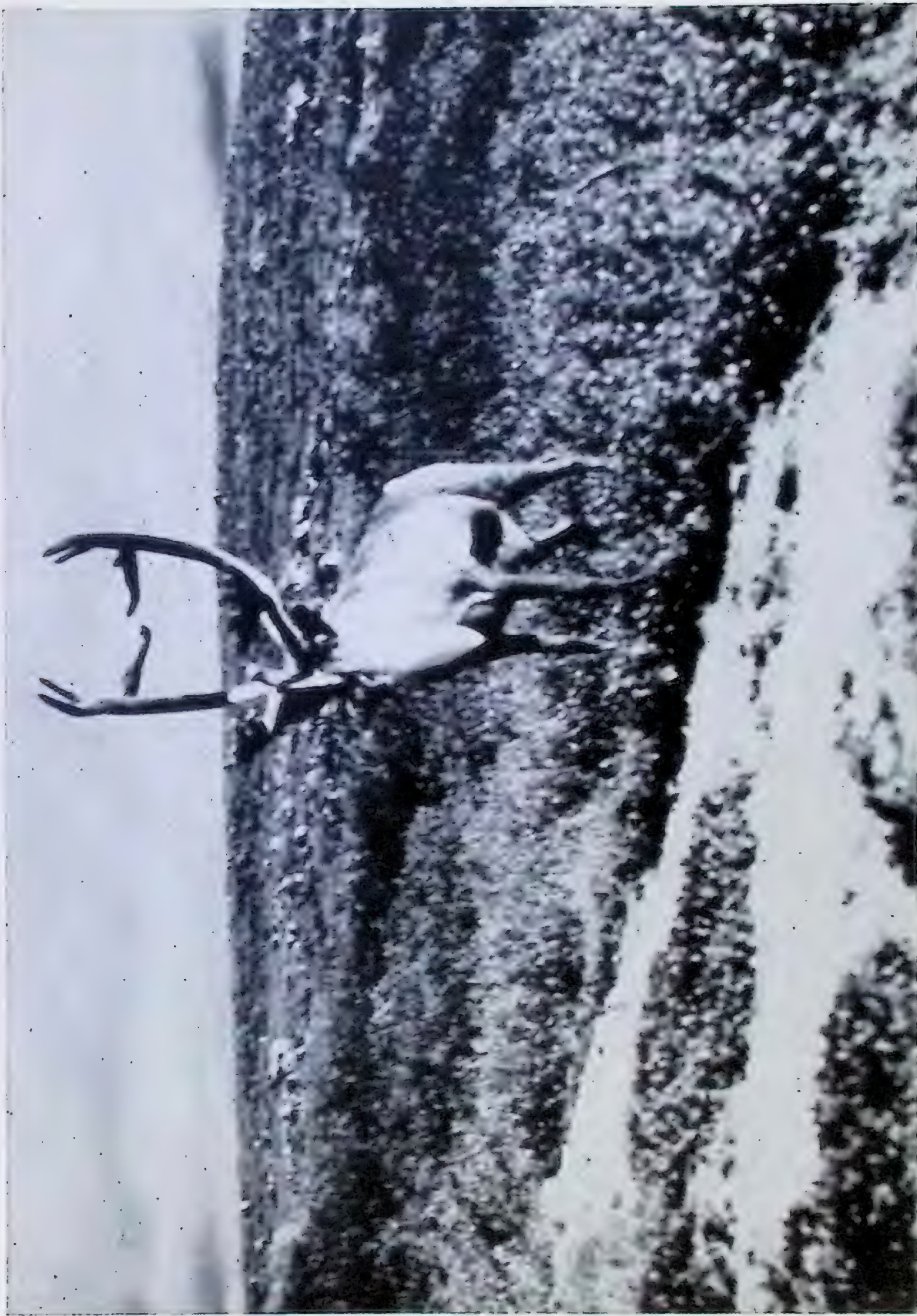
Adult males: basal length, 327.7 (307-346); orbital width, 163.4 (151-171); nasal length, 107.3 (76-125); post nares, 39.34 (36.0-42.5); tooth row, 90.05 (82.7-99.4); diastema, 120.5 (111-132); occipital height, 135.4 (125-160).

Adult females: basal length, 302.2 (283-333); orbital width, 152.1 (143-166); nasal length, 99.3 (78-122); post nares, 36.48 (31.7-41.5); tooth row, 87.89 (76.9-94.4); diastema, 110.3 (97-126); occipital height, 121.2 (110-133).

External Measurements

There is very little information available for the nominate race. Jacobi (1931) reported the total length to be about 200 cm, the shoulder height 130 cm, and the weight 120-150 kg for adult males. I measured one set of male hooves: length 80, width 80 mm; and one set of female hooves: length 78, width 65 mm. Generally speaking, the nominate race is of average size for the species. Degerbøl and Krog (1959) provide measurements of long bones.

Length of male metatarsus, 274 (270-278); male metacarpus, 198 (194-202); length of female metatarsus, 243 (240-245); female metacarpus, 173 (171-176).



—Photo by Canadian Wildlife Service

American tundra reindeer bull

Pelage

An adult male from Norway in late autumn coat (BM(NH) 81.9.28.2) may be described as follows: muzzle, Cartridge Buff; forehead, Snuff Brown; cheeks, Pinkish Buff; neck, Pinkish Buff; back, Tawny Olive; chest, Light Pinkish Cinnamon; belly, Cream; flank stripe, Pinkish Buff over Tawny Olive; legs, Sayal Brown on anterior surface, Cream behind.

An adult female from Norway in similar pelage (BM(NH) 83.7.28.1) may be described as follows: Muzzle, greyish; forehead, Buffy Brown; cheeks, Vinaceous Buff; neck, Avel-laneous; back, Bister; chest, Snuff Brown; flank stripe, Vinaceous Buff over Snuff Brown; belly, white; legs, Snuff Brown. There is a strong possibility that these skins had faded somewhat during the long course of museum storage.



FIGURE 4. Distribution of tundra reindeer (CYLINDRICORNIS) toward the close of the nineteenth century: a—*tarandus*, b—*groenlandicus*, c—*granti*, d—*pearyi*, e—*cogroenlandicus*, f—*platyrhynchus*. The black circles represent localities from which specimens were examined.

Distribution

The original range of the tundra reindeer included the entire mountain system of Scandinavia from Stavanger Fiord to North Cape, including the mountains of western Sweden (Dalecarlia, Särna, and Idre) and northern Finland north of Lake Inari (Jacobi, 1931, and Lonnberg, 1909).

The distribution in the Soviet Union has been outlined by Sokolov (1959). It included the treeline and tundra regions across northern Europe and Asia. Sokolov mentioned Murmansk Province (including the Kola Peninsula); Arkhangelsk Province tundra (in ancient times); Kolguyev, Vaygach, and Solovetskiye* islands; the Polar Urals; Yamal, Gydanskiy, and Taymyr peninsulas. They also migrated from the mainland to the offshore islands such as Belyy, Deer, Sibiryakova, Dikson, White, the Nordenskiöld Archipelago, Bolshevik Island (the southern Island of the Severnaya Zemlya group), and the New Siberian Islands—Lyakhovskiy, Kotelny, Faddeyevskiy, and Novaya Sibir—and even reached Bennet Island during regular annual migrations in the past. On the mainland they occurred in large numbers on the lower Lena River and across the tundra between the Yana and Indigirka. They were particularly abundant on the lower Kolyma River and in Eastern Siberia about 100 years ago. At present wild reindeer are rare in Eastern Siberia and are absent from the Taygonos Peninsula and Olyutorskiy district. There are no records from Wrangel Island.

It is extremely difficult to draw a southern boundary for *tarandus* distribution in northern Europe and Asia because of the overlap between the range of this form and the forest reindeer *fennicus* during annual migrations. There is also the matter of intergradation between the two subspecies. Such intergradation is recognized in southern Lapland and in eastern Siberia, but it probably occurs extensively elsewhere. This remains a problem that cannot be solved at this distance. Indeed I suspect that many more specimens would be required before such a study could be undertaken.

Status

Wildhagen (1952) reviewed the status of wild reindeer in Norway. Though exterminated in northern Norway soon after 1900, they remain in fair numbers in the mountains of southwestern Norway between Trondhjem and Stavanger. He made no estimate of the population, but the legal kill in 1950 was approximately 1,500 animals. Since the population seems to be at least holding its own, this suggests a population of 5,000 or more animals. According to Lonnberg (1909), native tundra reindeer were exterminated in Sweden soon after 1860 and in Finnish Lapland about 1900.

Tundra reindeer have been similarly reduced on the tundra of European Russia. Sokolov (1959) reported that they were increasing in the central part of the Kola Peninsula, east of the railway to Murmansk; however they were extinct on the tundra of Arkhangelsk Province. They still occur on Novaya Zemlya and on Vaygach Island. East of the Ural Mountains they occur on Yamal and Gydanskiy peninsulas near the coasts and on nearby islands.

Tundra reindeer are still to be found in fair numbers on the northern tundra of western Siberia. The Taymyr Peninsula is a stronghold, and they also occur between the Yana and Indigirka rivers. However they are less common in Eastern Siberia where they are still to be found in the headwaters of the Anyuy and Anadyr rivers. Everywhere native tundra reindeer are in constant competition with domestic reindeer herds in the northern portions of the Soviet Union (Sokolov, 1959).

* The Russian spelling of Place Names comes from The Times Atlas of the World, 2, Southwest Asia and Russia. The Times Publishing Company, London (1959).



FIGURE 5. Present distribution of tundra reindeer (CYLINDRICORNIS): a—*tarandus*, b—*groenlandicus*, c—*granti*, d—*pearyi*, f—*platyrhynchus*.

Taxonomic History

Linnaeus's primary reference for *Cervus tarandus* in the 10th edition of *Systema Naturae* was his own *Fauna Suecica*, 1746, which located the type locality in Sweden according to Thomas (1911). Lonnberg (1909) traced Linnaeus's Lapland travels and restricted the type locality to the districts of Dalecarlia, Särna, and Idre. He mentioned a series of skulls from Langfjället, Sweden, as being topotypes. Fortunately, these specimens were still available for study at the Naturhistoriska Riksmuseet, Stockholm.

Schreber (1784) introduced the name *sibiricus* for Siberian reindeer. Hollister (1912) restricted that type locality to the Ob', in the neighbourhood of the Berezovskiy Mountains. However, Ellerman and Morrison-Scott (1951) state that *sibiricus* Schreber is not a valid name, because the word was used to indicate the provenance of the particular reindeer illustrated. A number of authors followed with scientific descriptions of Siberian reindeer: *sibiricus* Murray (1866), *lenensis* and *asiaticus* Millais (1915), and *asiaticus* Jacobi (1931). The last name was based upon a domestic reindeer specimen.

In the meantime, believing that this step was necessary if Linnaeus's name stood for the species, various authors suggested additional subspecific names for the Scandinavian reindeer: i.e. *rangifer* Gmelin (1788), *typicus* Lydekker (1898), and *cylindricornis* Camerano (1902).

Based upon a single cranium with antlers, in the private collection of H. J. Pearson of Bramcote, Notts., United Kingdom, Lydekker (1903) proposed the name *pearsoni* for the native reindeer of Novaya Zemlya. The antlers were characterized by the heavy palmation of brow, bez, and terminal tines, and elongate posterior tines. Lydekker based his specific description on the single set of antlers and on the insular range of the form.

Jacobi (1931) placed *pearsoni* in the synonymy of *tarandus tarandus*, and later Sokolov (1937 and 1959) placed *sibiricus* under the synonymy of the nominate race.

Remarks

The specimens examined appear to represent only three important demes: European, Asian, and Novaya Zemlyan. The statistical analysis of the Eurasian demes is given in Tables 10 and 11. Sokolov (1937) concluded that the skulls of Siberian tundra reindeer were generally similar to the European tundra form but averaged slightly larger. The present analysis has confirmed that conclusion. The differences, however, are statistically insignificant. The antlers indicate about the same degree of variation. The pelage of the Siberian reindeer is reported to be slightly paler and longer than that of the European race (Flerov, 1933). However the differences are slight and subject to individual variation.

An adult male in early summer coat, taken on the east Siberian sea-coast on July 18, 1912 (ZIL 24470), may be described as follows: muzzle, silvery; face, Clove Brown; cheeks, Clove Brown; neck, Ecru Drab; back, Caetura Black; chest, Hair Brown (restricted); flank stripe, Drab Gray over Caetura; legs, anterior Fuscous stripe, paler behind; socks wide, mirror large, creamy white.

The Novaya Zemlyan reindeer are a little more distinctive than the Siberian. In the preliminary analysis of Eurasian populations it was found that the nasal length, diastema and occipital height measurements of females were significantly different from the measurements of European tundra reindeer; however, those of the males were not. The males were inseparable from *tarandus* in all characters except nasal length, in which they resembled *platyrhynchus*. It would not seem valid to recognize a subspecies in which only the females could be distinguished. The Novaya Zemlya reindeer appear to possess certain intermediate skull characteristics between *tarandus* and *platyrhynchus*. Compared with New World populations, the same fact might be interpreted slightly differently by saying that they possess certain skull characteristics, such as shorter nasals and rostrums characteristic of Arctic island reindeer populations.

Antlers are generally digitate and do not bear out the initial specific identification presented by Lydekker.

The pelage has been described as long and paler than *tarandus*, almost white in winter. A light rose-brown colour is present on the head and back, legs whitish, flank stripe lacking (Flerov, 1933). A male taken in 1883

(ZIL 589), in late winter pelage, may be described as follows: head, creamy with Buffy Brown cheek patches; neck, Ivory Yellow; back, Avellaneous; flank stripe, chest, and belly, Ivory Yellow; legs, Chamois stripe on inner hind side, Avellaneous on outer side.

The insular distribution of the form was one of Lydekker's points in recognizing *pearsoni*. However, later information has shown that the Novaya Zemlya reindeer may not have been so isolated. Harper (1945) mentioned that mainland tundra reindeer occasionally cross the Kara Strait to Novaya Zemlya in migration. Sokolov (1959) reported that native reindeer still occur on Vaygach Island between Novaya Zemlya and the mainland and that Kolguyev Island to the west was formerly inhabited. It seems likely that mainland tundra reindeer formerly migrated regularly in summer to those islands in much the same way as American tundra reindeer migrated to Victoria Island before human interference curtailed the movement.

Specimens Examined

A total of 71 specimens were examined from the following localities: NORWAY: 3 (BM(NH)), 2 (MCZ); Mountains of SW Norway, 5 (UOM); 'Lapland,' 2 (UKM); Bergen, 1 (USN); Fillefjell Mts., 2 (BM(NH)); Maristovo, 2 (USN); Morsvik, 1 (UCM). SWEDEN: Langfjallet, 3 (NRM); Swedish Lapland (no fixed locality), 3 (NRM). USSR: Kola Peninsula, 1 (UHM), 2 (LIZ); Novaya Zemlya, 1 (UCM), 12 (LIZ); Arkhangelsk Province, 1 (LIZ); Taymyr Peninsula, 5 (LIZ); Nordenskiöld Archipelago, 2 (LIZ); Yana River, 1 (LIZ); Verkhoyansk, 1 (UOM), 1 (LIZ); Indigirka River, 1 (UOM); Kolyma River, 1 (UOM); northern Siberia, 6 (LIZ); Markovo, Yakutsk, 1 (AMNH); Little Anyuy River, 1 (AMNH), 1 (USN); Cape Bolshoy Baranov, 1 (USN); Panteleikha, 1 (USN); New Siberian Islands, 3 (LIZ); Anadyr River, 4 (AMNH).

Rangifer tarandus groenlandicus (Linnaeus)

American Tundra Reindeer

1767. *Cervus tarandus* (Syn. *Capra groenlandica*) Linnaeus, System. Nat. 12 ed., 1: 98. (Alpine America.)
1780. *Cervus groenlandicus* Borowski, Gemeinnützige Naturgeschichte des Tierreichs,, 1(3): 72.
1780. *Cervus tarandus*, Fabricius, Fauna Groenlandica; 16, Kobenhavn.
1788. *Cervus tarandus* β *groenlandicus* Gmelin, Caroli Linne Syst. Nat., ed. 13, 1: 177. (Southwest Greenland.)
1829. *Rangifer tarandus* var. *arctica*, Richardson, Fauna Boreali-Americana, 1: 241.
1857. *Rangifer groenlandicus*, Baird, Mammals of North America, 634.
1877. *Rangifer groenlandicus*, Caton, The antelope and deer of America, 105.
- 1898-99. *Rangifer groenlandicus*, *R. arcticus*, Trouessart, Cat. Mamm. vivent. quam fossil. 2: 887-888, R. Friedlander & Sohn, Berolini.
1898. *Rangifer tarandus groenlandicus*, *R. tarandus arcticus*, Lydekker, The deer of all lands, etc., 33-49, Rowland Ward, London.
1902. *Rangifer groenlandicus*, *R. arcticus*, Grant, 7th Ann. Rept. N.Y. Zool. Soc., 24 pages.
1915. *Rangifer groenlandicus*, *R. arcticus*, Lydekker, Cat. Ung. Mamm. BM(NH), 2: 254, London.
1915. *Tarandus rangifer arcticus*, Millais, The gun at home and abroad, 4: 261-262.
1931. *Rangifer arcticus arcticus*, *R. tarandus groenlandicus*, Jacobi, Das Rentier: etc. Akad. Verslag. m. b. H.: 69, 78, Leipzig.
1935. *Rangifer arcticus arcticus*, Murie, North Am. Fauna, 54: 74. Washington.

1952. *Rangifer tarandus groenlandicus*, *R. tarandus arcticus* Flerov, Fauna of the USSR, Mammals, vol. 1, no. 2, Musk deer and deer, 246-247.
1959. *Rangifer tarandus arcticus*, *R. t. groenlandicus*, Hall and Kelson, The mammals of North America, 2: 1018, 1020.
1960. *Rangifer arcticus arcticus*, Manning, Arctic Instit. North America, Tech. Pap., 4: 47.

Type specimen. None designated.

Type locality. Southwest coast of Greenland.

Diagnosis and biology. As outlined under Group CYLINDRICORNIS.

Description

See Tables 12 and 13 and Figures 8 to 15 for a statistical comparison between the skulls of this subspecies and those of its neighbours.

Average Skull Measurements

Adult males: basal length, 334.1 (296-372); orbital width, 164.8 (146-183); nasal length, 108.2 (88-141); post nares, 38.74 (34.0-51.5); tooth row, 91.44 (78.2-103); diastema, 122.9 (101-140); occipital height, 137.7 (113-175).

Adult females: basal length, 296.9 (273-326); orbital width, 149.9 (142-159); nasal length, 97.7 (79-115); post nares, 34.22 (30.5-38.5); tooth row, 88.78 (78.3-99.0); diastema, 107.6 (93-122); occipital height, 120.6 (108-133).

External Measurements

Adult males (including data from Kelsall, 1957, Table 12): total length, 1,803 (1,600-2,096, n=58); shoulder height, 1,095 (872-1,180, n=31); hind foot, 520 (435-570, n=55); weight, 109.8 kg (80.7-153.3, n=16); length of hooves, 86 (78-95, n=9); width of hooves, 86 (65-95, n=9); antler length, 960 (520-1,270, n=30); antler spread, 752 (510-1,100, n=20); beam vertical diameter, 38 (27.5-57, n=17); beam horizontal diameter, 30 (21-41, n=17).

Adult females (including data from Kelsall, 1957, Table 13): total length, 1,664 (1,370-1,860, n=61); shoulder height, 1,043 (959-1,120, n=26); hind foot, 504 (432-561, n=60); weight, 80.7 kg (63.0-93.9, n=25); length of hooves, 80 (75-88, n=10); width of hooves, 84 (80-90, n=8); antler length, 390 (230-500, n=25); antler spread, 250 (170-350, n=10); beam vertical diameter, 19.6 (15-27, n=20); beam horizontal diameter, 13 (11-16, n=19).

Length of adult male metatarsus, 281 (274-290, n=11); metacarpus, 197 (190-206, n=11).

Length of adult female metatarsus, 258 (240-268, n=10); metacarpus, 183 (173-191, n=11).

Pelage

Comparison of pelage colour is handicapped by wide individual variation. Several comparable specimens are described below, according to Ridgway's (1912) colour standards, to permit appraisal of individual and seasonal variation. An adult male from Godthaab Fiord, southwest Greenland (topotype UCM 2727), in late summer pelage may be described as—muzzle, white; face, Olive Brown; neck, Pale Olive Buff; back, Clove Brown; chest, Bister (restricted); belly, Ivory Yellow; flank stripe, Tilleul Buff over Sepia; legs, Snuff Brown; socks, white. An adult male from Baffin Island taken on August 26 (NMC 5536), may be described as—nose, Bister; face, Snuff Brown; neck, Tilleul Buff; back, Clove Brown; chest, white; belly, white; flank stripe, Tilleul Buff over Olive Brown; legs, Bister forestripe, socks, target, poll, white. An adult female from the central Mackenzie District (NMC 14087), may be described as—nose, Bister; face, Snuff Brown; neck, Tilleul Buff; back, Fuscous; chest, Bister; belly, white; flank stripe, Tilleul Buff over Fuscous; legs, Bister.

The pelage becomes paler by winter. An adult female in worn winter coat from the Dolphin and Union Straits herd (NMC 2758) may be described as—nose, Bister; cheeks, Cartridge Buff; neck, Cartridge Buff; back, Hair Brown; chest, belly, and flank stripe, Cartridge Buff; legs, Snuff Brown; forestripe, paler behind; socks and mirror, wide white.

Distribution

In historical times reindeer have been known to occupy the unglaciated coastal strips of southwest Greenland from Cape Farewell to Upernavik. From medieval Icelandic manuscripts we have learned that a thousand years ago reindeer were numerous in the Julianehaab area and provided the early Norse settlers with meat and skins. Those herds became extinct on the restricted unglaciated coasts where the densest Norse settlements were, only to return after the Norse had vanished (Porsild, 1951). At the beginning of the nineteenth century reindeer were abundant from Upernavik to Frederikshaab, including Disko Island. Rink (1857) reported the annual kill was up to 37,000 in the 1820's. With the introduction of firearms the annual kill had dropped to about 1,500 at the close of the century (Porsild, op. cit.).

The distribution outlined in Figure 5 is that of about 1900, before the reindeer population had been seriously depleted by modern firearms. It included the following Canadian arctic islands: Baffin (Soper, 1928); Freuchen (1953) reported that hundreds of reindeer had drowned while migrating from Baffin Island to Bylot Island during the time of the Fifth Thule expedition, 1922-24; Southampton Island (Sutton and Hamilton, 1932); Coats Island, Mansel Island, Nottingham and Salisbury islands (Grant, 1902); Somerset, King William (Schwatka, 1885); and southern Victoria Islands (Stefansson, 1913); as well as Melville, Boothia, Adelaide, and Kent peninsulas.

The mainland distribution was bounded on the south by a line drawn through the following localities: ONTARIO: Fort Severn (Tyrrell, 1913), Little Sachigo Lake. MANITOBA, Island Lake, Cross Lake, The Pas. SASKATCHEWAN: Flin Flon, Stanley, Churchill Lake. ALBERTA: Clearwater River, Embarras Portage, and Lake Claire. On the west it was bounded by a line drawn through the following points: Mackenzie District, Wood Buffalo Park, Yellowknife, Fort Rae, Horn Mountains, Willowlake River, Johnny Hoe River, Keller Lake, Great Bear River, Smith Arm of Great Bear Lake, Colville Lake, Horton River to Franklin Bay (Banfield, 1954b).

Intergradation between *groenlandicus* and *caribou* occurs in the region between the Anderson River and the Mackenzie Delta. On the eastern boundary of the range of the subspecies, intergradation is indicated in northwestern Ungava Peninsula which was reached by immigrating reindeer "island hopping" across Hudson Bay via Southampton, Coats, and Mansel islands.

Status

Native reindeer are still to be found in small numbers in southwest Greenland from Upernavik district to Godthaab district, especially at the heads of the longer fiords (Degerbøl, 1957). They are absent from Disko Island. The distribution of reindeer in Baffin Island is now centred on the western side of the island where aerial surveys in 1954 indicated a population of about 5,000 animals. Other scattered herds are known to occur at the heads of fiords in the Pond Inlet and Clyde River regions. Miller (1955) thought the reindeer had been extirpated in 1943 on Bylot Island by hunting. However, Mr. L. M. Tuck of the Canadian Wildlife Service reported one old bull shot by Eskimos on the ice off the north coast near Cape Hay

during the winter of 1956-57. The population of Southampton Island is thought to be less than 25, and that of Coats Island to be about 100. Mr. W. E. Taylor of the National Museum of Canada, through interviews with Eskimos, learned that the reindeer were extirpated on Mansel Island about 1900, although there was a sight record of two near Swaffield Harbour about 1949 or 1950. He collected a series of skull fragments and bones which are referable to this race from archaeological sites on the Island. They are extinct on Nottingham and Salisbury islands. Specimens have been collected from the recently discovered Prince Charles Island in Foxe Basin. Flaherty (1918) reported the extirpation of the reindeer on the Belcher Islands about 1887, as a result of the tundra freezing during a prolonged sleet storm. Unfortunately, no local specimens have been collected so that the identity of the subspecies remains a mystery. Reindeer of this subspecies are probably on the verge of extinction on Victoria and King William islands. Manning (1960) has reviewed the extinction of the Dolphin and Union Strait herd which formerly migrated to southern Victoria Island until about 1920.

Within the past decade there has been a rapid decline in the population of reindeer on the continent between Hudson Bay and the Mackenzie River valley. The herds have withdrawn from the northern periphery of their range. They have become particularly scarce in northern Mackenzie and northern Keewatin districts but still occur in some numbers in the central portion of their range and locally in northern Keewatin District. The present population is estimated at 200,000 by Tener (1960).

Taxonomic History

Edwards (1743) was one of the earliest authors to name a New World reindeer population. His quaint figure 51 portrays a reindeer carrying antlers in velvet, labelled "Greenland buck" *Capra groenlandica* (See Plate II). Linnaeus first listed Edwards' name in synonymy under his *Cervus tarandus* in the 12th edition of *Systema Naturae* (1767) and added "Alpine America" to the range of his species. This is, therefore, the earliest valid name for the New World tundra reindeer subspecies, in view of the rejection of Brisson's (1762) names. There are a number of later references to the Greenland reindeer in the eighteenth century: Borowski (1780), Fabricius (1780), and Gmelin (1788). However, these names are junior homonyms of Linnaeus's (1767). The southwest coast of Greenland was the region visited by Europeans, and undoubtedly those early references pertain to the reindeer of that coast.

Richardson's *arcticus* has long been recognized as the name of the barren-ground caribou of Baffin Island and the tundra of Keewatin and Mackenzie District. Baird (1857) was the first to consider the relationship between *groenlandicus* and *arcticus*. He wrote (op. cit., p. 634) "It is a question, admitting this to be a distinct species, whether it should bear the name of *groenlandicus* or *arcticus*. Following the strict law of priority however I have retained the former, although objectionable on account of its local character." Caton (1877) followed Baird's lead and referred to American reindeer as *Rangifer groenlandicus*. Seton, writing at a much later date (1927, p. 100), echoed the same conclusion, "By all the rules then *groenlandicus* is the type of the American forms of the Arctic Reindeer and should be taken as the starting point. But it is so rare and little known that I make the well-known and abundant *arcticus* the subject of this Life,

and compare others with it." Lydekker (1898) re-established the Linnaean species *tarandus* and listed the two forms as subspecies.

Later American authors, from Grant (1902) to Manning (1960), separated the two populations into two full species more as a matter of convenience. The fundamental relationship was even more obscured by Jacobi (1931) who referred *groenlandicus* to the European species *tarandus*, and the Asian *sibiricus* to the American species *arcticus*, based upon the possession of the European antler "bend." Degerbøl (1957) has shown that this character is not a valid criterion to differentiate New World and Old World reindeer.

It was Ellerman and Morrison-Scott's (1951) and Flerov's (1952) insistence that all reindeer and caribou belong to a single species that caused a reappraisal of the American viewpoint (Hall and Kelson, 1959).

Remarks

In the preliminary analysis, eight geographic populations were studied from Greenland to the Mackenzie River of Canada. Eventually those were amalgamated to five demes which showed some geographic variation: southwest Greenland, Baffin Island, northern Keewatin and Southampton Island, the central tundra of Canada, and Dolphin and Union straits. Those demes showed no significant differences or clines but rather exhibited a mosaic type of variation. The Dolphin and Union straits deme was small and pale, indicating some *pearyi* influence (Manning, 1960). The northern Keewatin and Southampton Island animals were large and pale. The Baffin Island form was very small and darker. The Greenland animals were relatively large and dark, while the tundra *arcticus* was average in colour, size, and most other characters. Yet all these populations shared a great many common variable characters in antler formation, pelage pattern, and skull characters which indicated that they were fundamentally tundra reindeer and distinct from woodland caribou.

A secondary statistical analysis was conducted on three regroupings: southwest Greenland, northern Keewatin, and *arcticus*, as shown in Tables 14 and 15. It was found that the northern Keewatin deme was significantly different from *arcticus* at the 5 per cent level for the basal length and orbital width of males, and the basal length of females, but was not significantly different from the southwest Greenland form. None of the other characters indicated similar significant differences. The Dolphin and Union straits deme similarly could be shown to be significantly smaller than the northern Keewatin deme, yet the nearby Baffin Island reindeer were much smaller than the Dolphin and Union group but showed no influence of *pearyi* in shortened rostrum, hooves, or pale pelage.

All these demes exhibited local variations that are considered below the recognizable subspecific level in this revision. A similar level of variation is to be found in woodland caribou demes across North America as well.

The appraisal of the relationship between *arcticus* and *groenlandicus* has been hampered in the past by the lack of topotypes of *arcticus*. The collection of a number of specimens from near the type locality (Ross Lake, Walta Lake, Grant Lake, and Lever Lake, Mackenzie District) for the National Museum of Canada has greatly facilitated this study. Little difference has been found between the two forms.

The occurrence of three subspecies on Greenland is open to question. An explanation is found in the Greenland Ice Cap, which spills to the sea in a number of broad tongues that effectively divide the unglaciated coastal strips into virtual "islands." The distributions of *pearyi* and *groenlandicus* occupy two of these coastal strips opposite nearby populations of the respective subspecies on the Canadian Arctic Archipelago. Frozen Kennedy Channel offered a highway for the colonization of northwestern Greenland from Ellesmere Island, but Baffin Bay, 200 km wide between Cumberland Peninsula, Baffin Island, and Holsteinborg, southwest Greenland, appears to be a formidable barrier.

Dr. Christian Vibe of Copenhagen informed me of his studies of climatic cycles in Greenland. He believes that during short-term cold phases the East Greenland Ice sweeps around Cape Farewell and up the west coast to meet the southward-moving West Ice off Baffin Island. In winter the ice-flocs freeze to form an ice bridge. He believes both reindeer and Arctic foxes have crossed to Greenland on such an ice bridge. He interviewed an old Greenlander who had found caribou starving on the ice off the Greenland coast. The close resemblance between the two populations suggests the recent colonization of southwest Greenland from Baffin Island, perhaps repeatedly.

The relationship between *groenlandicus* and *caribou* is complicated by the annual migration in winter of tundra reindeer to the forested regions of Mackenzie District, Alberta, Saskatchewan, and Manitoba. The same region is occupied by scattered bands of woodland caribou. Although the ranges of the two races are sympatric at those periods, intergradation is unlikely because the normal rutting period has passed. In the spring the tundra reindeer herds may migrate up to 1,000 km back to their summer tundra habitat. During that brief period the two subspecies are sexually isolated and behave as sympatric species. In the Mackenzie Delta, northwestern Ungava, and possibly the Ontario-Manitoba boundary, where the autumn range is close to forested regions, intergradation has taken place between the two subspecies.

Specimens Examined

A total of 228 specimens from the following localities were examined during the study: SOUTHWEST GREENLAND: 4 (AMNH), 20 (UCN, measurements from Degerbøl 1957), 4 (NMC), 1 (MCZ), 1 (USN); Godthaab, 5 (UCM); Holsteinborg, 1 (AMNH), 4 (UK). CANADA: N.W.T., Franklin District; Baffin Island, Milne Inlet, 1 (UCM); Cumberland Sound, 5 (NMC); Pangnirtung Fiord, 11 (NMC); Pond Inlet, 2 (NMC); Nettilling Lake, 2 (NMC); Bowman Bay, 6 (NMC); Piling, 3 (NMC); Taverner Bay, 1 (NMC); Cape Albert, 1 (NMC); Prince Charles Island, 2 (NMC); Mansel Island, 3 (NMC); Coats Island, 1 (NMC); Southampton Island, 5 (CM); Southern Victoria Island, 1 (NMC); 1 (AMNH), 1 (BM(NH)); Keewatin District, northern Hudson Bay, 1 (AMNH); Wager Bay, 4 (AMNH), 6 (AMNH, measurements from Allen, 1908); Pelly Bay, 9 (NMC); Sherman Inlet, 9 (NMC); Baker Lake, 10 (NMC); Eskimo Point, 5 (NMC); Chesterfield, 1 (NMC); Beverly Lake, 5 (NMC); Nuelin Lake, 4 (AMNH), 1 (ROM); Edehon Lake, 1 (ROM); Seal Hole Lake, 1 (ROM); Aberdeen Lake, 2 (NMC); Mackenzie District, Thelon River, 4 (NMC); Artillery Lake, 2 (NMC); Fort Resolution, 1

(NMC); Clinton-Colden Lake, 1 (NMC); Aylmer Lake, 2 (AMNH), 1 (NMC); Contwoyto Lake, 1 (NMC); Hood River, 1 (NMC); Tree River, 1 (NMC); Ross Lake, 2 (NMC); Walta Lake, 1 (NMC); Aurora Lake, 1 (NMC); Grant Lake, 2 (NMC); Lever Lake, 1 (NMC); Norman Lake, 1 (NMC); Great Bear Lake, 1 (AMNH); Horton River, 2 (AMNH); Dease River, 2 (AMNH); Kater Point, 1 (NMC); Bernard Harbour, 13 (NMC); Dolphin and Union straits, 1 (NMC); Langdon Bay, 1 (AMNH); Darnley Bay, 1 (AMNH); Manitoba, Duck Lake, 5 (NMC); South Indian Lake, 3 (ROM); McClintock, 4 (CM); The Pas, 1 (UBC); Saskatchewan, Camsell Portage, 6 (NMC); Cree River, 2 (NMC); Cree Lake, 2 (NMC); Lake Athabasca, 3 (NMC); Williams Lake, 1 (NMC); Stony Rapids, 11 (NMC); Hacking Lake, 1 (NMC).

Rangifer tarandus granti J. A. Allen

Grant's Reindeer

- 1902. *Rangifer granti* J. A. Allen, Bull. Am. Mus. Nat. Hist., 16: 119-127.
- 1902. *Rangifer granti*, Grant, 7th Ann. Rept. N.Y. Zool. Soc., p. 5.
- 1912. *Rangifer excelsifrons* Hollister, Smithson. Misc. Coll., 56 (35): 5. (Meade River, near Point Barrow, Alaska.)
- 1915. *Tarandus rangifer granti*, Millais, The gun at home and abroad, 4: 266.
- 1915. *Rangifer tarandus granti*, Lydekker, Cat. Ungulate Mamm. in the BM (NH). London. p. 253.
- 1935. *Rangifer arcticus granti*, Murie, North Am. Fauna, 54: 80.
- 1952. *Rangifer tarandus arcticus*, Flerov, Fauna of the USSR. Vol. 1, no. 2: Musk deer and deer, p. 247.
- 1959. *Rangifer tarandus granti*, Hall and Kelson, Mammals of North America, Ronald Press, New York, 2: 1020.

Holotype. Adult male collected by Andrew J. Stone on October 29, 1901, No. 17593, American Museum of Natural History, skin and skull.

Type locality. Western end of Alaskan Peninsula, opposite Popoff Island, Alaska, U.S.A.

Description

See Tables 12 and 13 and Figures 8 to 14 for a comparison between the skulls of this subspecies and those of its neighbours.

Average Skull Measurements

Adult males: basal length, 349.7 (346-354); orbital width, 166.2 (162-169); nasal length, 120.2 (117-126); post nares, 40.65 (40.3-41.0); tooth row, 96.85 (90.5-102.7); diastema, 126.7 (123-130); occipital height, 144.2 (139-153).

Adult females: basal length 306.2 (295-325); orbital width, 153.3 (144-159); nasal length, 103.3 (95-116); post nares, 36.30 (35.0-38.2); tooth row, 90.00 (84.9-98.1); diastema, 108.7 (102-120); occipital height, 125.7 (117-134).

External Measurements

Adult males: total length, 1,834 (1,727-1,880, n=5); shoulder height, 1,114 (992-1,245, n=5); hind foot, 566 (542-584, n=5); length of hooves, 100; width of hooves, 83; tail, 203; antler length, 912 (720-1,300, n=8); antler spread, 814 (660-1,080, n=8); beam vertical diameter, 38; beam horizontal diameter, 28.

Adult females: total length, 1,657 (1,651-1,664, n=2); shoulder height, 916 (903-929, n=2); hind foot, 527 (521-533, n=2); antler length, 386 (280-470, n=4); antler spread, 311 (240-380, n=4); beam vertical diameter, 15; beam horizontal diameter, 10.5.

Pelage

The coat of the type specimen of an adult male in late autumn pelage may be described as follows: muzzle, whitish; nose, Bister; cheeks, Sayal Brown; neck, Pale Pinkish Buff; back, Verona Brown; flank stripe, Pale Pinkish Buff (restricted); chest, Snuff Brown; belly, white; legs, Snuff Brown; target, fairly large, and socks creamy white and fairly wide. The females are paler (Allen, 1902a).

Distribution of Typical Population

The Alaska Peninsula from Lake Clark and Lake Iliamna to the tip, northward along the coast of Bristol Bay, at least as far as Nushagak, Unimak, Unga, Amak, and Deer islands (Murie, 1959). It is possible that Kodiak Island was occupied by this race at one time. Kellogg (1936, p. 37) reported caribou bones in native midden sites on the Island, and Jacobi (1931, p. 82) cites Kadiak, Alaska. The University of Kansas Museum of Natural History has a specimen (No. 2264) reported from "Kadiak, Alaska," in 1896. However, Clarke (1958) does not include the species in his list of the Island's mammals. Clarke informed me in a letter that Kadiak was the Russian name for the Island but suggested that the University of Kansas specimen probably came from the Alaskan or Kenai peninsulas since caribou meat and antlers are still brought to the Island from the Alaska Peninsula. The Kansas specimen indeed seems to be a woodland caribou from the Kenai Peninsula.

At present the caribou of the Alaskan Peninsula are isolated from the interior herds; however, this was not originally the case. Murie (1935) published a letter from E. W. Nelson, which reads in part: "In the years not far antedating my arrival at St. Michael in 1877, caribou occurred practically all along the coast of Bering Sea of Alaska from Norton Sound to the Peninsula except in limited areas, such as the delta of the Yukon and some of the marsh areas between Yukon and Kuskokwim . . . I am convinced that the caribou of the peninsula were in contact with those farther north but may have been sufficiently isolated to form a local race." Leopold and Darling (1953, p. 55) report that the peninsula herds used to migrate toward the mainland and that the mainland herds migrated as far down as Lake Iliamna until those movements were interrupted by the placement of 10,000 or more domestic reindeer in the area.

Status

The introduction of domestic Siberian reindeer to Alaska after 1891 and the eventual abandonment and straying of reindeer herds (Leopold and Darling, 1953) greatly influenced the fate of native caribou on the Alaska Peninsula. Murie (1959, p. 331) published extracts from a letter of David L. Spencer, supervisor of Kenai National Moose Range, concerning caribou populations in 1958. He reported approximately 150 animals on Unimak Island and 5,000 on the Alaska Peninsula. However, because of extensive interbreeding with domestic reindeer, most of those are believed to be hybrids. Many observers express doubts as to the survival of *granti* as a pure stock.

Taxonomic History

Allen (1902a) described the race of caribou inhabiting the tundra of the Alaska Peninsula as a distinct species of the barren-ground group of caribou, related to *arcticus* and *groenlandicus* but not closely related to *stonei* of the nearby Kenai Peninsula. He wrote (op. cit., p. 127): "The external and

cranial differences between *granti* and the various forms of the woodland caribou are so great in almost every respect that no detailed comparison is necessary" (! author). Although he reported a series of 15 paratypes, his tables list only seven adults, and later examination has shown that two of those were less than four years old.

Hollister (1912) described *excelsifrons* from near Point Barrow on the Arctic coast of Alaska. It is generally conceded (Murie, 1935, pp. 77-78) that Hollister picked as a type an unusually small skull with an exceptionally high cranium. That character is not shown in other skulls from the same locality.

A reprint of Hollister's paper in the Mammal Section, National Museum of Canada, has the following pertinent footnote to page 5, in R. M. Anderson's handwriting: "O. J. Murie in 'Alaska—Yukon Caribou,' North American Fauna 54, 1935, pp. 76-78 places *excelsifrons* as a synonym of *Rangifer arcticus stonei* Allen (1901)—I examined the type and other specimens from Point Barrow in Washington in ——— [year left blank] and told N. Hollister, Allan Brooks, and Chas. Sheldon who were present that the type specimen was abnormal and that *excelsifrons* was a good race compared with typical *Rangifer arcticus* from east of the Mackenzie on size, etc., but not on characters given by Hollister—R.M.A. 1941."

From this quotation and from Allen's original description it is evident that these authors considered the Alaska Peninsula race to be a tundra reindeer and not closely related to the woodland caribou represented by *stonei* in Alaska. The present study has shown that tundra caribou of the Alaska Peninsula and the Brooks Range of northern Alaska resemble each other closely. Although *granti* is generally slightly larger, the differences are not statistically significant.

Later authors—Millais (1915), Lydekker (1915), and Murie (1935)—reduced the form to subspecies rank under the tundra reindeer, *tarandus* or *arcticus*. Murie (1935, p. 81) wrote: "Comparison of available material from Alaska Peninsula and study of data on early distribution corroborate this conclusion: the peninsula herds have been sufficiently isolated to form a local race, but the differences are not striking."

Jacobi (1931, p. 76) listed *granti* as a species in the synonymy under *arcticus* Richardson. He included Alaska in the range of *arcticus arcticus* (op. cit., p. 82) only on the basis of the occurrence of "reindeer" in the widest sense, including reports of doubtful value of the local races *excelsifrons*, *granti*, and *stonei*. He did not consider it advisable to handle those forms' distributions separately in a faunistic context. However, later he listed *R. a. excelsifrons* (p. 84) and *R. a. stonei* (p. 89) but omitted any further reference to *granti*, in spite of reference to its distribution on page 82. Flerov (1952) seems to have followed Jacobi's analysis and considered *granti* as a synonym of *arcticus*.

Remarks

It was necessary to pay particular attention to the locality and date of capture of specimens from the typical range of this subspecies in order to discard any specimens that might have been stray domestic reindeer or reindeer-caribou hybrids. This selection unfortunately reduced the number of specimens for study. Only the type series and later specimens mentioned by Murie (1935) were used.

The identification of the caribou populations in Alaska and in the Yukon district has been the most difficult problem in the present investigation. Originally, nine geographic groups were analysed in the region. Those groups were gradually amalgamated, as statistical analyses indicated that the differences were insignificant. Eventually four groups remained exclusive of the Kenai and Alaska peninsula groups, which have been previously treated. Those were as follows: the Nelchina herd, the Steese Highway herd, the northern Yukon herd, and the Brooks Range herd. Specimens from Forty Mile, west central Yukon, were placed with the Steese Highway herd on the basis of field reports. The statistics for those Alaska-Yukon demes are presented in Tables 20 and 21. South to North clines are evident in most characters treated. It should be noted that the reindeer of northern Yukon are close to *caribou* range in the Mackenzie District. Other factors, such as pelage colour, external measurements, and antler formation, bear out the same clines. Subsequent statistical analysis indicated that the Brooks Range population could not be separated adequately from *groenlandicus*, and the southern groups could not be separated from *granti*.

Previous taxonomic studies have been reviewed fully under the woodland caribou and in the present section to support the present conclusions that contact between the various Alaskan populations was more extensive formerly and that the various populations differed only slightly. Those assumptions point to a final conclusion that caribou populations in Alaska and Yukon Territory indicate a broad belt of intergradation between the woodland caribou, *caribou*, and the tundra reindeer, *groenlandicus*.

Since the only statistically valid Alaskan race is *granti* of the Alaskan peninsula, one is faced with the possible choice of referring to all central and northern Alaskan populations as *granti* intergrades.

Specimens Examined

A total of 12 specimens of the typical form from the following localities: Unimak Island, 1 (MCZ); Urilea Bay, Unimak Island, 4 (USN); Alaska Peninsula, opposite Popoff Island, 5 (AMNH); Muller Bay, Alaska Peninsula, 2 (AMNH).

Intergrades between *granti*, *groenlandicus*, and *caribou*: a total of 81 specimens from the following localities: ALASKA: Canoe River, 2 (AMNH); Rainey Pass, 1; Beechey Pt., 1 (AMNH); Pt. Moller, 1 (AMNH); Alaska Range, 2 (MCZ); Anaktuvik Pass, 11 (NMC); Brooks Range, 1 (NMC); Tulugak Creek, 5 (NMC); Tulugak Lake, 2 (USN); Steese Highway, 4 (NMC); Forty Mile, 3 (NMC); Taylor Highway, 2 (NMC); Lake Louise, 1 (NMC); Susitna River, 4 (NMC); Richardson Highway, 1 (NMC); Tyrone Creek, 2 (NMC); Glen Highway, 2 (NMC); Oshetna Creek, 2 (NMC); Eureka, 1 (NMC); Denali Highway, 1 (NMC); Savage River, 1 (USN); Mount McKinley, 1 (USN); McCarthy, 1 (USN); Eagle, 2 (USN); Kogaluk River, 1 (USN); Rampart House, 2 (USN); Meade River, 1 (USN); Ophir, 5 (USN); Caro, 3 (USN). YUKON TERRITORY: Old Crow, 1 (USN); Forty Mile road, 7 (NMC); Clinton road, 1 (NMC). NORTHWEST TERRITORIES: Mackenzie District, Mackenzie Delta, 3 (NMC); Holmes Creek, 1 (NMC); Aklavik, 1 (NMC); Anderson River, 1 (NMC).

Rangifer tarandus pearyi J. A. Allen

Peary Reindeer

1902. *Rangifer pearyi* J. A. Allen, Bull. Am. Mus. Nat. Hist., 16: 409 (Northeast Ellesmere Island, 79° N. lat., N.W.T.).
1902. *Rangifer pearyi*, Grant, 7th Ann. Rept. N.Y. Zool. Soc., 24 pages
1931. *Rangifer pearyi*, Jacobi, Das Rentier: Akad. Verslag. m. b. h.: 111.
1952. *Rangifer tarandus pearyi*, Flerov, Fauna USSR Mammals, vol. 1, no. 2: Musk Deer and Deer, 246.
1959. *Rangifer tarandus pearyi*, Hall and Kelson, The Mammals of North America, 1020.
1960. *Rangifer arcticus pearyi*, Manning, Arctic Inst. North America, Tech. Paper 4, 47.

Holotype. Skin, adult male, No. 19231, American Museum of Natural History. Collected by R. E. Peary on June 15, 1902. Skin in poor condition, untanned, lacking feet and left front leg.

Type locality. East coast of Ellesmere Island, at approximately 79° N. lat., N.W.T., Canada.

Diagnosis. Small size; short, pointed muzzle; velvet, grey; antlers, bone-coloured, often lacking lateral divergence, digitate; pelage, long, silky, creamy-white in early winter, summer coat slate above, lacking pronounced flank stripe, white below; legs, white except for narrow frontal stripe; hooves, extremely short and broad.

Description

See Tables 12 and 13 and Figures 8 to 15 for statistical comparisons between the skulls of this subspecies and those of its neighbours.

Average Skull Measurements

Adult males: basal length, 304.6 (279-343); orbital width, 157.7 (145-169); nasal length, 99.1 (81-120); post nares, 35.65 (31.6-42.4); tooth row, 93.13 (80.3-106); diastema, 106.1 (94-128); occipital height, 129.1 (117-152).

Adult females: basal length, 265.4 (257-272); orbital width, 142 (134-149); nasal length, 86.1 (76-96); post nares, 31.58 (29.6-35.5); tooth row, 87.69 (78.0-93.0); diastema, 90.5 (86-93); occipital height, 111.9 (105-119).

External Measurements

Adult males: total length, 1,668 (1,330-1,860, n=23); hind foot, 499 (459-540, n=22); length of hooves, 78.3 (74-81, n=7); width of hooves, 84.7 (80-94, n=7); weight, 110 kg for one adult specimen; antler length, 928 (640-1,140, n=14); antler spread, 603 (420-840, n=13); beam vertical diameter, 37 (28.5-45, n=12); beam horizontal diameter, 28.2 (20-34, n=12); metacarpus length, 168 (184-198, n=11); metatarsus length, 265 (251-290, n=13).

Adult females: total length, 1,361 (1,054-1,650, n=3); hind foot, 480 (465-495, n=3); length of hooves, 64.5 (60-70, n=4); width of hooves, 80 (70-85, n=4); weight, 52.6 kg; antler length, 342 (230-500, n=9); antler spread, 212 (170-270, n=7); beam vertical diameter, 19.8 (16-24, n=9); beam horizontal diameter, 12.8 (10.5-17.0, n=9); metacarpus length, 172 (1).

Pelage

The original describer and many later authors have emphasized the long silky white coat of the present subspecies which is only worn during the winter. The summer coat is short and dark, generally similar to other races. Furthermore, other races of reindeer become almost white in late winter. Typical specimens of this subspecies may be characterized as slate-coloured rather than Clove Brown above, lacking a prominent flank stripe, and white below. The annual change in pelage may be described by the following series of male hides from the Queen Elizabeth Islands, Canadian Arctic Archipelago.



Perry reindeer bulls
—Photo by S. D. MacDonald, Nat. Mus. Canada.

Fresh autumn pelage (NMC 21727): face, Drab Gray; neck, Pale Smoke Gray; back, Drab Quaker Gray; chest, white; belly, white; flank stripe, Pale Smoke Gray; legs Drab anterior stripe, otherwise white. Late autumn pelage (NMC 2764): nose, brown; cheeks, Ivory Cream; neck, Ivory Yellow; back, Deep Olive Buff; chest, Ivory Yellow; belly, white; flank stripe, Ivory Yellow; legs, anterior Bister stripe, otherwise white. Winter coat (NMC 1255): nose, cheeks, neck, Ivory Yellow; back, Drab; chest, white; belly, Ivory Yellow; no flank stripe; legs, Light Pinkish Cinnamon anterior stripe, otherwise white. A female taken on April 9 (NMC 8798) in worn winter coat was completely white except for an Avellaneous coloured saddle over the rump.

Distribution

Northwestern Greenland north of Inglefield Bay; the Queen Elizabeth Islands of the Canadian Arctic Archipelago, including Ellesmere. (Although Degerbøl (1957) suggests reindeer are more common on the east coast of Ellesmere Island, actually most of the reindeer range is on the west coast.) Axel Heiberg, Devon, Cornwallis, Bathurst, Melville, Prince Patrick, Mackenzie King, Borden, Ellef Ringnes, and other smaller islands. South of Viscount Melville Sound, Barrow Strait, and Lancaster Sound, this race is found on Banks, northwestern Victoria, Prince of Wales, and Somerset islands. The occurrence of this subspecies on eastern Baffin Island, as indicated by Hall and Kelson (1959, p. 1019), is without foundation.

Status

The Peary reindeer has probably been less affected by human interference than any other subspecies, because its distribution is largely north of recent Eskimo habitation. The journals of some of the explorers, particularly Stefansson and Peary, suggest that reindeer were fairly abundant on some islands. Today, reindeer still occupy much the same range as when first encountered. However, their numbers are not large, nor do they seem to increase even though they are seldom molested. In addition, large numbers of carcasses of this subspecies, which had apparently died of natural causes, have been found. These facts suggest the conclusion that the sparse range is presently stocked at its carrying capacity.

Unfortunately, as this subspecies has not received adequate attention, little published information is available concerning its biology, ecology, and status. The following estimated populations for various islands has been gathered mostly from unpublished reports of A. H. Macpherson of the Canadian Wildlife Service, Ottawa: Melville Island, 3,000; Prince Patrick, 1,300; Emerald, 400; Mackenzie King, 900; Borden, 1,200 (Macpherson, 1959); Banks, 4,000 (Manning and Macpherson, 1958); Prince of Wales, 500 (Manning and Macpherson, 1959); Ellesmere Island, 500 (J. S. Tener, verbal); Loughheed, 300 (E. F. Roots, verbal); Ellef Ringnes, fairly common but not so many as Prince Patrick (S. D. MacDonald, verbal); Cornwallis Island, 25 (Thorsteinsen, verbal).

Taxonomic History

Glover (1960) has recently shown that Pennant's (1787, p. 51) brief description of a white deer skin that was presented to the Hudson's Bay Company was condensed from Andrew Graham's manuscript journal from Fort Churchill about 1774 or 1775. It seems that the skin was presented by Matonabee, Samuel Hearne's Chipewyan guide to the Coppermine River in 1771-72. He probably secured it in trade from Coppermine River Eskimos who may have secured the skin on Victoria or Banks islands. Thus it seems

that a specimen of the race was secured and reported as early as 1787. Many English explorers to the Canadian Arctic Archipelago in the nineteenth century reported native reindeer, but the form was not described until 1902, when J. A. Allen (1902b and 1908) based his description on a large series of specimens obtained by Commander R. E. Peary from Ellesmere Island.

This well-marked form was generally granted specific rank by earlier authors. Flerov (1952) reduced it to subspecific rank upon his conclusion that all reindeer were members of the same species *tarandus*. Manning (1960) proved intergradation of *pearyi* with the American barren-ground caribou and indicated *pearyi* as a subspecies of the New World *arcticus*.

Remarks

The typical characteristics of this race are rather constantly exhibited in the insular populations of the Queen Elizabeth Islands. Free interchange of populations among the islands across frozen straits has been observed in a few cases and is clearly indicated in many others.

The Banks Island population on the average shows intergradation with the mainland tundra reindeer; however, it is more closely related to *pearyi*. An adult bull from Banks Island in early autumn coat (NMC 21161) may be described as follows: nose, Hair Brown; cheeks, Light Drab; neck, Drab Gray; back, Caetura Drab; flank stripe, Tilleul Buff; chest and belly, white; legs, buff except for Drab anterior stripe. Most of the specimens clearly show the *pearyi* affinity, but a few from De Salis Bay on the south coast show skull characteristics of *groenlandicus*. The National Museum of Canada has a specimen from the herd which crossed Amunsden Gulf during the winter of 1951-52, taken at Cape Dalhousie, which clearly shows its *pearyi* affinities. The inclusion of northwestern Victoria Island in the range of the subspecies is based upon Eskimo reports and aerial surveys but is, unfortunately, not substantiated by specimens.

The Prince of Wales Island population is unique in that it possesses all the diagnostic characters such as shortened rostrum, high cranium, and pale pelage, yet it is much larger than typical *pearyi*. There are no significant signs of intergradation with *groenlandicus* in the series. One might argue that the Island has a more favourable environment than the more northern islands, which have promoted the greater growth. However, Banks Island at the same latitude and with a more luxuriant tundra vegetation supports smaller reindeer. The Prince of Wales Island reindeer suggest the occurrence of a "super" *pearyi* deme. In view of the nearby occurrence of typical *groenlandicus* on the Boothia and Adelaide peninsulas, it is suggested that the two contiguous populations are exhibiting character displacement as outlined by Brown and Wilson (1956). According to Eskimo and European reports, Peary reindeer cross between Prince of Wales and Somerset islands. On the latter Island they are reported at Stanwell-Fletcher Lake. However, mainland tundra reindeer are reported occasionally to stray to southern Somerset Island and even to Prince of Wales Island in summer. They are reported not to intermingle with the resident Peary reindeer (Macpherson, 1959).

The Inglefield Bay population of northwest Greenland is isolated both to the north and south by tongues of the Greenland Ice-cap, which reach

the sea at Melville Bay and Kane Basin. Although Melville Bay is a formidable barrier, yet the specimens indicate some influence from *groenlandicus* of southwestern Greenland. The Inglefield caribou are larger, darker, with longer, less-pointed rostrums and more widely spreading antlers. The opposite coast of Ellesmere Island is also glacier-clad and must support a sparse reindeer population. This may explain why the gene flow across the north end of Baffin Bay (ca. 150 km) has not been so dominant as one might expect.

An adult bull from Orluks Fiord, northwest Greenland, taken on September 3 (UCM 2708), may be described as: muzzle, white; cheeks, Sayal Brown; neck, Pale Pinkish Cinnamon; back, Sayal Brown; chest and belly, white; flank stripe, Cream Buff over Light Pink Cinnamon; legs, Tawny Olive forestripe, buffy behind; antlers, white; velvet, cream.

A comparison of the statistics of skull measurements for the Arctic Island forms is provided in Tables 16 and 17.

Specimens Examined

Typical *pearyi*—75 from the following localities: NORTH GREENLAND: 2 (AMNH—R. E. Peary). NORTHWEST TERRITORIES: Ellesmere Island, Black Cliff Bay, 10 (AMNH); Grant Land, 5 (AMNH); Porter Bay, 2 (AMNH); Lake Hazen, 7 (AMNH), 1 (MCZ); Mount Pullen, 1 (NMC); Cape Lockwood, 1 (UCM); Otto Fiord, 1 (UCM); Fram Fiord, 2 (NMC); Hilgard Bay, 1 (NMC); Fosheim Peninsula, 1 (NMC); Craig Harbour, 2 (NMC); Starnes Fiord, 1 (ROM); Axel Heiberg Island, 6 (UCM); Ellef Ringnes Island, Isachsen, 3 (NMC); Bathurst Island, Erskine Inlet, 10 (NMC); Graham Island, 1 (NMC); Lougheed Island, 1 (NMC); Mackenzie King Island, 1 (NMC); Allison Inlet, Melville Island, 2 (NMC); Prince Patrick Island, Mould Bay, 5 (NMC), 2 (USN); Prince of Wales Island, Browne Bay, Ommanney Bay, 7 (NMC).

Intergrades *pearyi* x *groenlandicus*, a total of 38 specimens from the following localities: NORTHWEST GREENLAND: Inglefield Bay, 2 (UCM); Marshall Bay, 1 (UCM); Orluks Fiord, 1 (UCM). NORTHWEST TERRITORIES: Banks Island, 2 (NMC); Sachs Harbour, 3 (NMC); De Salis Bay, 2 (NMC); Castel Bay, 3 (NMC); Storkenson Bay, 1 (NMC); Cape Kellett, 6 (NMC); Kellett River, 1 (NMC); Thomsen River, 2 (NMC); Sea Otter Bay, 8 (NMC); Big River, 2 (NMC); Egg River, 2 (NMC); Lennie River, 1 (NMC); Mackenzie District, Cape Dalhousie, 1 (NMC, migrant). These hybrids resembled *pearyi* more closely.

Rangifer tarandus eogroenlandicus Degerbøl

East Greenland Reindeer

1957. *Rangifer tarandus eogroenlandicus* Degerbøl, Acta Arctica, Fasc. 10, p. 5. København.

1959. *Rangifer tarandus eogroenlandicus*, Hall and Kelson, Mammals of North America, vol. 2, p. 1019, Ronald Press, New York.

Holotype. Mounted skin with antlers, skull, some leg bones, male collected on Ryder Expedition, 1891–92, CN 647, University of Copenhagen Zoological Museum.

Type locality. Hekla Havn, Danmarks ø. South of Milne Land at head of Scoresby Sound, East Greenland.

Diagnosis. Very small pale reindeer, antlers white, normally spread, with slender round beams, usually digitate, but terminal tines often palmate; tooth rows and nasals shorter than *pearyi*.

Description

Average Skull Measurements

Adult male skulls: basal length, 275.0 (264–290); orbital width, 147.7 (139–157); nasal length, 86.7 (81–97); post nares, 34.07 (31.5–36.3); tooth row, 89.92 (86.5–95.0); diastema, 89.0 (87–91); occipital height, 120.5 (104–137).

Adult female skulls: basal length, 253; orbital width, 138; nasal length, 80; post nares, 33.2; tooth row, 79.5; diastema, 92; occipital height, 111.

External Measurements

Males: Antler length, 1,013 (695–1,170, $n=10$); spread, 935 (690–1,305, $n=10$) (Degerbøl, 1957); beam vertical diameter, 24 (21–31, $n=3$); beam horizontal diameter, 15 (13–16, $n=3$); white, generally digitate with frequent palmations.

Pelage

Known only from two hides which were taken at an unknown season. They are coarse and dirty white which suggests they were taken in spring.

Male: metatarsus length, 239 (235–246, $n=4$); metacarpal length, 171 (168–174, $n=3$); females: metatarsus, 220; metacarpal, 158.

Frequently, comments are made comparing the silkiness of certain hides to the coarseness of others without reference to season. Hides of *pearyi* are usually described as silky, which they are in early winter. However, by late spring all hides are somewhat coarser because of the breaking off of the long guard-hairs.

Distribution

East Greenland shoreline; known in life from Germania Land, 77° N. lat. to Scoresby Sound, 70° N. lat. During the Middle Ages extended as far south as Angmagssalik, 66° N. lat. according to remains in middens. Picked-up antlers from Pearyland may be referable to this form or, more likely, an intergrading population with *pearyi*.

Status

Extinct since about 1900.

Remarks

Degerbøl postulated that American tundra reindeer reached north Greenland and then differentiated into *cogroenlandicus* and *pearyi* in marginal habitat and *groenlandicus* in the more hospitable habitat of southwest Greenland.

The present investigation has indicated that *cogroenlandicus* and *pearyi* are much more closely related and that *groenlandicus* of southwestern Greenland is indistinguishable from the American tundra form *arcticus*. The taxonomic and historical evidence supports the conclusion that the ancestors of *pearyi* and *cogroenlandicus* survived the last Wisconsin glaciation in a refugium north of the continental glaciers in the western Queen Elizabeth Islands and perhaps in Pearyland, north Greenland.

Degerbøl suggests that a recent cold cycle (1850–1900), coupled with wolf predation and competition with musk-oxen, may have led to the extermination of the form.

I suspect that genetic drift in the small population may have reduced the viability of the form so that it was unable to cope with changing environment and succumbed much as did *dawsoni*.

Specimens Examined

A total of nine from the following localities: GREENLAND: Keiser Franz-Josef Land, 3 (MCZ), 2 (NRM); Scoresby Sound, 2 (UCM); Skibshaven, 2 (UCM).

In addition, a few useful measurements were taken from Degerbøl (1957, Table 9) of three skulls not examined.

Rangifer tarandus platyrhynchus (Vrolik) Spitsbergen Reindeer

1829. *Cervus (Tarandus) platyrhynchus* Vrolik, Nieuwe Verhandl. Kron. Nederl. Inst., 1 Klasse, pt. 2, p. 160 ("Lappland"?).
1863. *Cervus tarandus* forma *spetsbergensis* Andersén, Öfvers. Vet. Ak. Forhandl., 19: 457 (Spitsbergen).
1866. (*Rangifer arcticus*) var. *spitzbergensis* Murray, Geogr. Distrib. Mammals, pp. 155, 334.
1902. *Rangifer spitzbergensis* Camerano, Mem. R. Acad. Sci. Torino, ser. 2, 51: 159. 1900-1901.
1912. *Rangifer platyrhynchus*, Miller, Cat. Mamm. West Europe, 985 BM(NH) London.
1926. *Rangifer tarandus spetsbergensis*, Wollebaek, Resultater Norske Statsunderstøttede Spitsbergen—expeditioner, Bd. 1, nr. 4, 1.
1931. *Rangifer platyrhynchus*, Jacobi, Das Rentier, p. 73, Akad. Verslag. Leipzig.
1951. *Rangifer tarandus platyrhynchus*, Ellerman and Morrison-Scott, Checklist of Palaearctic and Indian Mammals. BM (NH), London, p. 375.
1952. *Rangifer tarandus platyrhynchus*, Flerov, Fauna of USSR: Mammals, Tom. 1, no. 2, Musk deer and deer, p. 244.

Holotype. None designated.

Type locality. Spitsbergen.

Diagnosis. Small pale reindeer with extremely short legs. The distal extremities of the nasal bones are expanded laterally; the supraorbital foramina usually lie in a groove; occipital condyles are narrow (Degerbøl, 1957).

Biology. Tundra habitat, gregarious polygamous, rut in early October (Wollebaek, 1926).

Description

Average Skull Measurements

Adult males: basal length, 288.1 (271-313), orbital width, 150.5 (141-160); nasal length, 89.6 (70-102); post nares, 33.73 (31.0-38.5); tooth row, 88.56 (82.7-95.8); diastema, 97.1 (87-104); occipital height, 119.4 (110-129).

Adult females: basal length, 253.9 (241-266); orbital width, 137.1 (130-143); nasal length, 71.5 (62-82); post nares, 29.40 (28.8-30.3); tooth row, 85.15 (78.4-90.0); diastema, 83.6 (78-90); occipital height, 107.7 (100-111).

External Measurements

Wollebaek (1926) and Lønø (1959) provided measurements. Average adult male measurements: total length, 1,450 (1,350-1,550, $n=4$); shoulder height, 887 (820-940, $n=6$). Adult females: total length, 1,290 (1,200-1,450, $n=6$); shoulder height, 820 (750-880, $n=7$); length of hooves, 75; width of hooves, 72. Antlers are ivory-coloured, digitate, with slender beams. Three bulls' antlers averaged 790 (680-850) in length and 680 (580-790) in greatest spread. The mean beam vertical diameter was 36 (33-38.5), and the mean beam horizontal diameter was 29 (25-33.5).

A female set of antlers measured 460 in length, 380 in spread, and the beam vertical diameter was 21, while the beam horizontal diameter was 16. Length of metatarsus of unknown sex, 205 (197-213); length of metacarpus of unknown sex, 152.

Pelage

An adult male skin taken on August 19, 1910, in the University of Helsinki Zoological Museum was described: muzzle, white; nose, Fuscous; cheeks, Olive Brown; neck, Pale Smoke Gray; back, Benzo Brown; flank stripe, Tilleul Buff over Olive Brown; chest, white; belly, white; legs, Hair Brown, stripe restricted to fronts of legs; socks, Ivory.

The late winter coat is described as long, woolly, and whitish.

Distribution

The islands forming the Spitsbergen Archipelago.

Status

Until the latter part of the last century, reindeer were distributed in fair numbers throughout the Archipelago (Wollebaek, 1926). However, during the early part of this century they were more heavily utilized by trappers and miners. Harper (1945) reported that the total protection provided by the Norwegian Government after 1925 permitted the population to increase. Lønø (1959) reported the present population of the Archipelago to total about 1,500 animals: on Nordaustlandet, 300–400; on Liefdefjorden and Reinsdyrfløya, 200–300; between Isfjorden and Van Mijenfjorden, 200; on Edgeøya, 500–600; and on Barentsøya, 150. The present distribution is plotted on Figure 5. According to Lønø about 15 per cent of the area is suitable reindeer pasture.

Taxonomic History

The Spitsbergen reindeer has for a long time been recognized as a distinct form. The type locality of Vrolik's *platyrhynchus* was questioned formerly, and Andersén's *spetsbergensis* was used extensively in the literature. However, since Miller (1912) established Spitsbergen as the type locality of Vrolik's name, based upon more exact references to location elsewhere in his report, *platyrhynchus* has been generally recognized as the name of the form.

Remarks

The Spitsbergen reindeer constitute a well-marked population exhibiting little variation. Their distinctions indicate a long period of isolation or the Sewell-Wright effect of genetic drift in a small isolated population. The Spitsbergen Archipelago was probably colonized by a very small number of migrants.

The problem arises whether to treat the form as a distinct species as do Miller (1912), Jacobi (1931), Flerov (1933), and Sokolov (1937), or as a geographic subspecies of *tarandus*, as Flerov (1952) and Ellerman and Morrison-Scott (1951) have done. I have chosen to follow the latter authors in that regard.

The authors who regard the form as a species point to its many distinctive features, such as extremely small size, pale coloration, short rostrum, relatively large teeth, distally-expanded nasals, and the supraorbital foraminal trench. Those factors may appear unique in comparison with its Palaearctic neighbours *tarandus* and *fennicus*. However, they are less unique when considered with Holarctic reindeer races and other island forms in general. Small size and short rostrum are characters associated with insular populations of cervids, and if you add long silky pale pelage you may add the additional refinement, Arctic islands. The Spitsbergen reindeer shares

those characters with *pearyi* and *cogroenlandicus* of the Nearetic islands. The relatively large teeth are similarly associated with the shortening of the facial region and are found in the Nearetic forms as well. The slender digitate antlers are indicative of its relationship with tundra reindeer.

If the Spitsbergen reindeer were a true species, one would expect to find a morphological discontinuity in the over-all variation within the genus. The distally-expanded nasal bones would appear to suit this criterion. However, during the current study two specimens—NMC 24326 from Pelly Bay, Keewatin District, Northwest Territories of Canada, and NRM 1412 from northwestern Finland—were found to have typically distally-expanded nasals, and several other specimens had slight variation of that character. It would appear, therefore, that the character is represented by a rare gene in the species, which found phenotypic expression in the isolated Spitsbergen population.

The last character of the supraorbital foramen trench was found randomly, but rarely, distributed in the many skulls studied including NMC 24326.

Wollebaek (1926) and Lønø (1959) cited several records of Samoyed domestic reindeer having strayed across the polar ice from Novaya Zemlya via Franz-Josef Land to Spitsbergen. Jacobi (1931) and Harper (1945) were doubtful of the evidence and considered the distances involved (380 and 340 km) too great for the migrants to have survived. However, Gordon (1922) and Lønø (op. cit.) accepted the immigration. In one case a reindeer that was shot bore a gull's foot tied to one antler. The Samoyeds of Novaya Zemlya are known to so decorate their reindeer in certain rituals. Reindeer bones are also known from Franz-Josef Land (Bruce and Clarke, 1899). And so the rare immigration of reindeer to Spitsbergen seems confirmed in spite of the adverse ocean currents and great distance. Elsewhere reindeer were known to cross from the New Siberian Islands to Bennet Island, a distance of 125 km, and from Banks Island to Cape Bathurst, a distance of about 185 km (Manning and Macpherson, 1958).

In any event, whether accidentally or with the aid of man, domestic reindeer reached Spitsbergen. They were reported to have joined the ranks of the native reindeer, possibly interbreeding with them. Wollebaek (op. cit., p. 60) wrote: "After its immigration into Spitsbergen the reindeer have perhaps in a short time got the distinctive features they [wild native reindeer] possess on this isolated island group, lying as it does on the outer limits of the habitat of this species." Again he wrote (op. cit., p. 61): "Some of the marked draught reindeer from Norway which Nordenskiöld brought with him to Spitsbergen during his expedition in 1872, escaped as soon as they were put ashore. In the summer of 1875 some of them were shot by hunters. The draught animals grazed along with the wild reindeer and were, like these, very fat." Intergradation is implied from the above-quoted remarks, an indication that domestic reindeer and Spitsbergen reindeer are only geographical subspecies of a single species. Lønø (op. cit.) reported that domestic reindeer were imported on at least three occasions during the nineteenth century. The sex of the importations is not known, but since they were mostly draught animals, the majority were probably castrated males which would make hybridization highly questionable.

Specimens Examined

A total of 20 from the Spitsbergen Archipelago, 1 (AMNH), 1 (BM(NH)), 2 (LIZ), 7 (NRM), 3 (UHM), 4 (UOM), 2 (UCM). In addition, measurements of one specimen from Trondhjem Museum and six from Tromsø Museum, published by Wollebaek (1926), were used in the tables of measurements.

GROUP COMPRESSICORNIS Jacobi 1931. WOODLAND
CARIBOU OR FOREST REINDEER

Diagnosis. Antlers, dark mahogany brown, generally short and heavy, beams flattened, often ridged; brow, bez and terminal tines usually palmate; terminal tines may be weakly developed, posterior tine usually close to bez tine; 30 to 40 per cent of females naturally antlerless; skull generally long and rugose, nasal bones long and narrow, particularly the distal portions, nasals arched and pinched posteriorly, rostrum elongate, occiput flattened and broad, orbits not protruding, post nares wide, tooth rows long, with ridges of bone posterior to M3, mandibles long and slender; body large, legs long, hooves large and moderately pointed, muzzle broad, tarsal gland large and oval, antler velvet dark brown; pelage generally dark chocolate brown, rump mirror small, socks usually narrow, and white on belly usually restricted.

Habitat. Bogs, swales, and alpine tundra in boreal coniferous forested regions. Depend upon arboreal lichens for winter food to a large extent.

Biology. Only moderately gregarious; live in small bands. Undertake local seasonal migrations, often altitudinal; individually more wary; polygamous. Usually one mature bull collects and serves a harem; rut commences in late September; parturition occurs in late May.

Rangifer tarandus caribou (Gmelin) American Woodland Caribou

- 1788. *Cervus tarandus* γ *caribou* Gmelin, Linn. Syst. Nat., ed. 13, 1: 177 (Quebec City, Que., Canada).
- 1829. *Rangifer tarandus* var. β *sylvestris* Richardson, Fauna Boreali Americana, 1: 250. (60 miles inland from Hudson Bay, Manitoba, and Ontario.)
- 1847. *Cervus hastalis* Agassiz, Proc. Boston Soc. Nat. Hist., 2: 187.
- 1856. *Rangifer caribou* Audubon and Bachman, The Quad. of North America, 3: 111-124. (St. Lawrence River region, Labrador and Maine.)
- 1896. *Rangifer terraenovae* Bangs, Prelim. Desc. Newfoundland caribou: 1-2, Boston, Nov. 11. (Codroy, Newfoundland.)
- 1896. *Rangifer terraenovae* J. A. Allen, Bull. Am. Mus. Nat. Hist., 8: 233. Nov. 21. (Grand Lake, Newfoundland.)
- 1898. *Rangifer tarandus caribou* and *R. t. terrae-novae* Lydekker, The deer of all lands, etc., Rowland Ward, London: 33-49.
- 1899. *Rangifer montanus* Seton-Thompson, The Ottawa Nat., 13(5): 129-130, Aug. 1899. (Illecillewaet watershed near Revelstoke, British Columbia.)
- 1901. *Rangifer stonei* J. A. Allen, Bull. Am. Mus. Nat. Hist., 14: 143, May 28, 1901, Kenai Penn., Alaska.
- 1902. *Rangifer osborni* J. A. Allen, Bull. Am. Mus. Nat. Hist., 16: 146. Apr. 16, 1902. (Cassiar Range of B.C.)
- 1902. *R. terraenovae*, *caribou*, *montanus*, *osborni*, *stonei* Grant, The caribou, 7th Ann. Rept. N. Y. Zool. Soc., 24 pages.
- 1912. *Rangifer fortidens* Hollister, Smithsonian. Misc. Coll., 56 (35): 3. Feb. 7, 1912 (Smoky River, Alta.), and *R. caribou sylvestris* (Richardson).
- 1914. *Rangifer arcticus caboti* G. M. Allen, Proc. New England Zool. Club, 4: 103-107. Mar. 24, 1914. (30 miles north of Nachvak fiord, Labrador.)



American woodland caribou bull and cow

—Photo by Kyle M. Walker

1915. *Rangifer tarandus caribou*, *R. t. sylvestris*, *R. t. terraenovae*, *R. t. montanus*, *R. t. stonei*, *R. t. fortidens*, *R. t. osborni*, Lydekker, Cat. Ung. Mamm. BM(NH), 4: 238-256. London.
1915. *Tarandus rangifer keewatinensis* Millais, The gun at home and abroad, etc., 4: 257. London. (North of Prince Albert, Sask.)
1915. *Tarandus rangifer labradorensis* Millais, op. cit., 259. (Lake Michikamaw, Cape Chidley, Nain, Davis Inlet, Labrador to Fort Chimo, Quebec.)
1915. *Tarandus rangifer ogilvyensis* Millais, op. cit., 263. (Ogilvy Mts., Yukon Territory.)
1919. *Rangifer mcquirei* Figgins, Proc. Colo. Mus. Nat. Hist., 3(1): 1. Dec. 28, 1919. (White River, Y.T.)
1931. *Rangifer arcticus stonei*, *R. a. osborni*, *R. a. montanus*, *R. a. fortidens*, *R. caboti*, *R. caribou caribou*, *R. c. sylvestris*, *R. c. terraenovae*. Jacobi, Das Rentier, etc., Akad. Verlag., pp. 89-122, Leipzig.
1935. *Rangifer montanus sclousi* Barclay, Proc. Zool. Soc. London, 1935: 305-307. (South fork Macmillan River, Y.T.)
1935. *R. arcticus caboti*, *R. a. stonei*, *R. a. osborni* Murie, North Am. Fauna, 54: 74-81. Washington.
1952. *R. tarandus caribou*, *R. t. terraenovae*, *R. t. caboti*, *R. t. montanus* Flerov, Fauna of the USSR, vol. 1, no. 2, Musk deer and deer, pp. 246-247.
1959. *Rangifer tarandus caboti*, *R. t. caribou*, *R. t. fortidens*, *R. t. montanus*, *R. t. osborni*, *R. t. stonei*, *R. t. sylvestris*, *R. t. terraenovae*. Hall and Kelson, The Mammals of North America, 2: 1018-1021.

Holotype. None designated.

Type locality. Quebec City, Quebec, Canada.

Description

See Tables 12 and 13 and Figures 8 to 15 for comparison of statistics of skull measurements between this subspecies and its neighbours.

Average Skull Measurements

Males: basal length, 374.3 (342-427); orbital width, 175.5 (157-198); nasal length, 131.4 (103-163); post nares width, 46.27 (38.0-56.2); tooth row, 97.40 (85.7-110); diastema, 140.0 (125-166); occipital height, 155.2 (131-188).

Females: basal length, 333.4 (306-368); orbital width, 159.3 (140-174); nasal length, 116.9 (92-143); post nares width, 40.88 (34.8-43.9); tooth row, 95.24 (82.5-107.4); diastema, 124.2 (108-139); occipital height, 131.6 (113-147).

External Measurements

Males: total length, 2,176 (1,905-2,472, n=19); hind foot, 625 (580-660, n=19); shoulder height, 1,289 (1,081-1,398, n=11); weight, 179.2 kg (161.0-226.8, n=5); length of hooves, 113.5 (100-135, n=14); width of hooves, 98 (75-118, n=14); antler length, 921 (350-1,580, n=57); antler spread, 733 (230-1,460, n=49); beam vertical diameter, 43.7 (19-105, n=34); beam horizontal diameter, 30.8 (13-52, n=34). Length of metatarsus, 316 (307-325); metacarpus, 230 (228-233).

Females: total length, 1,870 (1,730-2,045, n=11); hind foot, 582 (555-600, n=11); shoulder height, 1,225 (1,210-1,245, n=2); weight, 132 kg (100-152.5, n=3); length of hooves, 100 (95-105, n=5); width of hooves, 83.6 (75-95, n=5); antler length, 395 (210-610, n=31); antler spread, 298 (146-485, n=25); beam vertical diameter, 23.4 (15.5-35.0, n=24); beam horizontal diameter, 15.7 (11.0-25.0, n=24).

Pelage

The fresh autumn pelage of an adult bull (NMC 4800, Mount Albert, Que., Sept. 17) may be described as follows: muzzle, Pale Olive Buff; face, Fuscous, inside ears and crown with a sprinkling of white hairs; neck, Tilleul Buff; back, Clove Brown; flank stripe, Tilleul Buff (restricted); chest, Fuscous; belly, Tilleul Buff, (restricted); legs, Fuscous; socks, white, narrow; tarsal gland oval, Tilleul Buff 70 mm long; velvet, dark brown.

The similar coat of an adult female (NMC 4802, Mount Albert, Que., Sept. 17) may be described as follows: muzzle, Pale Olive Buff; face, Clove Brown; neck, Drab Gray; back, Clove Brown; flank stripe, Wood Brown; chest, Olive Brown; belly, Tilleul Buff; legs, Mummy Brown; socks narrow; tarsal gland, oval, 70 mm long; velvet, dark brown.

Distribution

The distribution outlined below is that at about the close of the nineteenth century, before the caribou population was curtailed by the expanding European population in North America. It will be observed to approximate the distribution of Boreal Forest in North America.

Woodland caribou originally inhabited the whole of the island of Newfoundland. Prichard (1910) mentioned three centres of abundance: the Humber River valley, the central portion of the island south of the railway, and a small herd on the Avalon Peninsula. Dugmore (1913) estimated the population at approximately 150,000 animals. Audubon and Bachman (1856) reported that caribou occasionally crossed the frozen Strait of Belle Isle in winter from Labrador to the Northern Peninsula of Newfoundland, where they often remained. This report has been repeated by later authors without any recent evidence of such a movement. Caribou, although much reduced in numbers, are still to be found in the Northern and Avalon peninsulas and the Humber valley, but the centre of abundance is on the tundra-clad highlands between the railway and the south coast.

Caribou once occurred on Prince Edward Island, according to Adams (1873). They were distributed throughout peninsular Nova Scotia, Cape Breton Island, and New Brunswick in fairly large numbers (Smith, 1940, and Morris, 1948), but under continual hunting pressures the populations declined and the range shrank to the northward.

The southern boundary of caribou distribution passed through central Maine from a coastal point near the head of Penobscot Bay westward to central Oxford County (Grafton, 20 miles northwest of Bethel, G. M. Allen, 1904). In northern Maine, caribou were once fairly abundant, particularly around Mount Katahdin, which was their last stronghold in the State (Palmer, 1938). They also occurred in extreme northern New Hampshire where caribou were reported at the Connecticut Lakes by Norton (1885) and Jackson (1922). They were reported also from extreme northeastern Vermont in the early part of the nineteenth century by Emmons (1840). Caribou were not known to have occurred in New York state in recent years (DeKay, 1842, and Merriam, 1884).

In the Province of Quebec, south of the St. Lawrence River, woodland caribou were originally distributed in the Appalachian Mountain region east of a line joining Lake Memphremagog and Three Rivers (Baird, 1859). North of the St. Lawrence the whole of the vast Quebec-Labrador peninsula was occupied by woodland caribou or woodland-tundra intergrades in western Ungava along the Hudson Bay coast. Although exact data are wanting, caribou were probably absent from the upper St. Lawrence River valley and the lower Ottawa Valley as far north as Mattawa, Ontario.

The whole of northern Ontario was occupied by caribou north of a line from Mattawa, Lake Nipissing, to Georgian Bay. Manitoulin Island was occupied according to DeVos and Peterson (1951) as was northwestern Ontario, north of Lake Superior and the Rainy River.

In Michigan, caribou occupied the northern part of the Lower Peninsula and the whole of the Upper Peninsula, the islands in St. Marys River, northern Lake Michigan, and Isle Royale in Lake Superior (Burt, 1948). The range was continuous along the southern shore of Lake Superior, across northern Wisconsin (La Point and Ashland), according to Cory (1912).

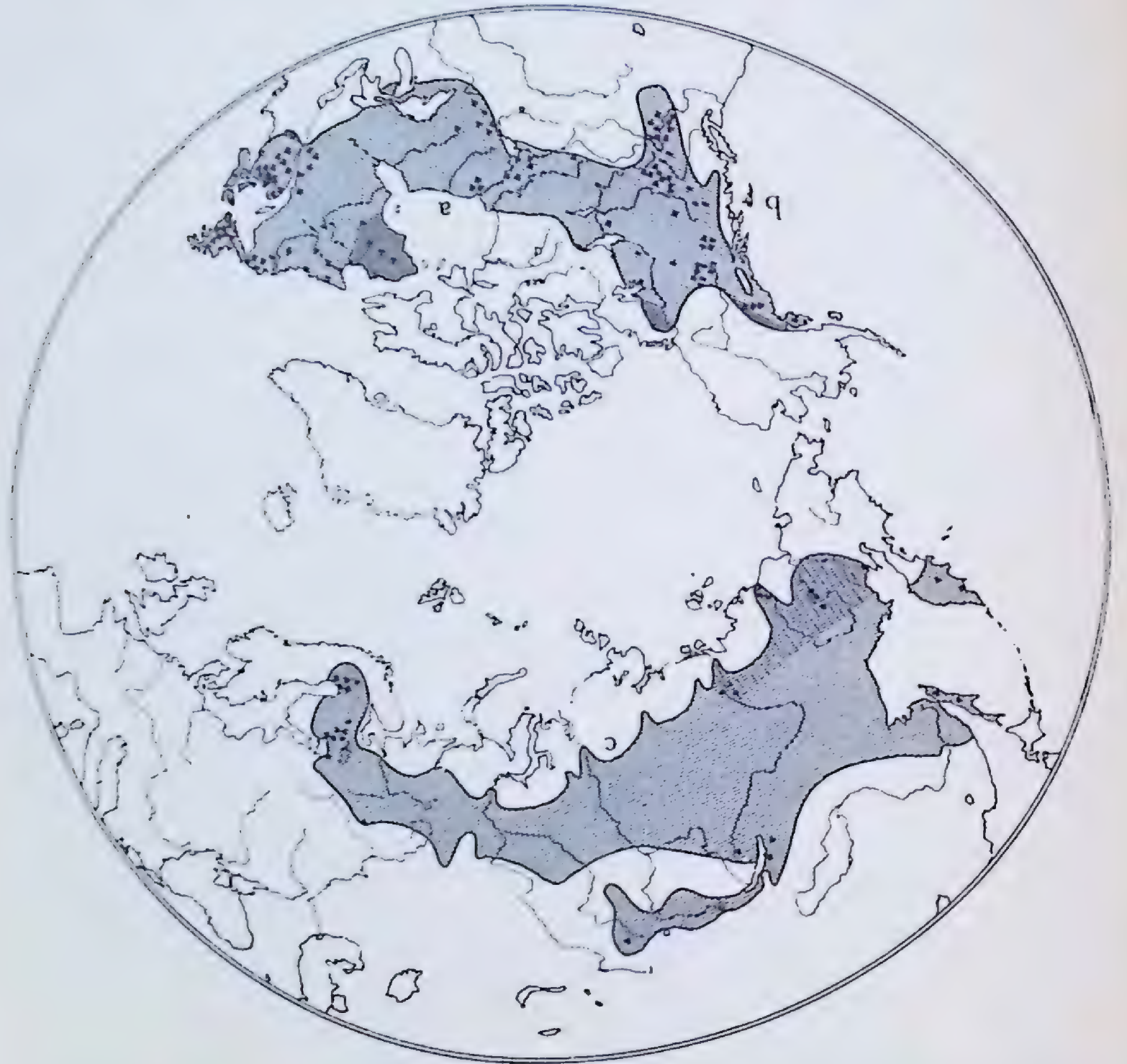


FIGURE 6. Distribution of woodland caribou and forest reindeer (*COMPTONICORNIS*) toward the end of the nineteenth century: a—*caribou*, b—*dawsoni*, c—*fennicus*. The black circles represent localities from which specimens were examined.

The history of caribou in Minnesota has been outlined by Swanson, Surber, and Roberts (1945). The original range included the Boreal Forest region in the northeast portion of the State from Kanabec County to Roseau County, west of Lake of the Woods. Early reports indicated that they were well distributed in this region when the early Europeans arrived about the beginning of the nineteenth century.

Upon reaching the Great Plains Region of central North America the caribou southern boundary turned northward along the western boundary of the Precambrian Shield. There are records of woodland caribou antlers

found in the Turtle Mountains, North Dakota, but it is difficult to know whether they indicated recent or prehistoric occupation of the area (Bailey, 1926, and Riis, 1938). In southern Manitoba, caribou were restricted to the eastern bog areas of the Whiteshell Forest Reserve, north to Lake Winnipeg, thence along its eastern and northern boundaries to the Interlaken district, then to the Pasquia Hills in eastern Saskatchewan. The northern boundary is difficult to define because of possible intergradation between woodland and tundra caribou along the Hudson Bay coast from Cape Tatnam to Cape Churchill. However, typical woodland caribou inhabit the valleys of the Churchill, Nelson, and Hayes rivers and occur sparingly across the northern part of the province to the Reindeer Lake area.

In Saskatchewan the southern boundary probably ran from near the town of Hudson Bay in the east to the region north of Prince Albert and then followed the southern border of the coniferous forest to Meadow Lake and Cold Lake on the Alberta boundary. The whole northern area of the Province was included in the range of woodland caribou with the possible exception of the taiga-tundra ecotone in extreme northeastern Saskatchewan. An early observation of woodland caribou in northern Saskatchewan was made at Cree Lake by Tyrrell (1896).

All of northern Alberta was formerly included in the range north of a line from Cold Lake to the bog area, 50 miles north of Edmonton, westward to the Athabasca River valley near Whitecourt and Edson. In the Rocky Mountains of western Alberta the range swept southward along the eastern slopes, at least as far as the upper Clearwater Valley in Banff National Park. South of that point the range seems to have been restricted to the western slopes of the Rocky Mountains in historical times; perhaps the western slopes provided more moisture for arboreal lichen growth. Lord (1866) reported woodland caribou in the Cascades and west slope of the Rocky Mountains in southern British Columbia.

The best succinct account of the distribution of caribou in British Columbia is provided by Cowan and Guiguet (1956). Caribou may now be found in the Rocky Mountains of eastern British Columbia from the Peace River south to Thompson Pass. In former times they probably occurred as far south as the Flathead Valley in eastern British Columbia. Seton (1927) reported them in the Flathead Valley of Glacier National Park, Montana. They also occupy the Selkirk and Monashee mountains from the upper loop of the Fraser River south to the International Boundary. The race is found also on the eastern slopes of the Coast Range from Morice Lake south to the Itcha and Cariboo mountains. In northern British Columbia caribou are distributed from the Omineca Mountains and from the Skeena and Sikanni Chief rivers northward to the Yukon boundary.

The range of the present form extends northward from the 60° parallel into the Mackenzie District, Yukon Territory, and Alaska. In the Mackenzie Valley the range extends eastward as far as the Nonacho Lake (Ingstad, 1933) and Fort Reliance (Clarke, 1940). This form is absent from the northeast shore of Great Slave Lake from Fort Reliance to Fort Rae but fairly common along the southwestern shores. From Fort Rae, the eastern boundary extends north along the Camsell River to the south and west shores of Great Bear Lake. Woodland caribou reach their northernmost range near Lake Colville, the upper Anderson River (MacFarlane, 1905),

and the lower Mackenzie River valley south of Arctic Red River. Caribou in the lower Anderson River and Eskimo Lakes areas are intergrades between woodland and tundra reindeer. The range of this form includes the river valleys emptying into the Mackenzie River from the northern Rocky Mountains to the west and the Liard River valley.

Recognizable woodland caribou occur in southern Yukon from the St. Elias Mountains in the west to the Liard River system in the east. The caribou that occupy the central and northern mountains are intergrading populations between the forest and tundra forms.

In Alaska this subspecies as a recognizable form was restricted to the southeastern portions of the State from the Kenai Peninsula to the Copper River Valley and the southern Alaskan "pan-handle." Caribou from central and northern Alaska are also intergrades.

Woodland caribou reached their southern limit in the Cordilleran region in the northwest Pacific coast states. Seton's (1927) reference to them in Glacier National Park, Montana, probably indicated their eastern boundary. Cooper (1868) reported caribou antlers by the road near Missoula, Montana. Merriam (1891, p. 80) reported that caribou occurred as far south as Elk City, Idaho, on the Clearwater River in 1872. In Washington State, Taylor and Shaw (1929) reported that caribou formerly occurred in the northeastern section "south to Usk and west to Okanogan County."

Status

At the present time woodland caribou populations have been greatly reduced in the southern portions of their range, and the southern limits of their distribution have been pushed northward.

The present Newfoundland population is thought to be approximately 5,000 to 6,000 animals. The caribou were exterminated in peninsular Nova Scotia in 1912 and on Cape Breton Island about 1925 (Anderson, 1938). In 1939, nine cow and two bull Newfoundland caribou were introduced to the Liscomb Game Sanctuary (Tufts, 1939). However, within a few years the transplanted animals had disappeared (Cameron, 1958, p. 39). Woodland caribou were exterminated in New Brunswick about 1927 (Anderson, 1938). They were extinct on Prince Edward Island prior to 1873 (Adams, 1873).

In Maine, Palmer (1938) concluded that the caribou had vanished about 1908. However, he later reported (Palmer, 1949) the observation of a bull caribou on the Maine-Quebec border in 1946. The species remains unreported in New Hampshire after 1881 and in Vermont after 1840.

The Shickshock Mountains of the Gaspé Peninsula, Quebec, remain the only stronghold of woodland caribou south of the St. Lawrence River. There, Moisan (1956-57) has estimated a population of 1,000 animals. North of the St. Lawrence, caribou have been extirpated south of a line drawn approximately from the Saguenay River to the southern tip of James Bay. The present population in the Ungava-Labrador peninsula is thought to be about 6,000 to 10,000 animals (Banfield and Tener, 1958). The centre of abundance is along the Quebec-Labrador boundary; only a few hundred are thought to remain in western Ungava.

"Woodland caribou currently occur right across northern Ontario, in the west, south to a line from Minaki to Savant Lake to the Black Bay

Peninsula of Lake Superior, and in the east, south to a line from Pukaskwa on Lake Superior to Swastika . . . The total estimated caribou populations of forest districts in Ontario was 7,200 in 1953-54." (Cringan, 1957.) By 1960, the population was reported to have increased to about 10,000, according to a communication from H. L. Lumsden, Ontario Department of Lands and Forests.



FIGURE 7. Present distribution of woodland caribou and forest reindeer (*COMPRESSIONIS*): a—*caribou*, b—*dawsoni*, c—*fennicus*.

The last caribou in Michigan were observed on the ice off Isle Royale in Lake Superior in the spring of 1905 (Riis, 1938). They disappeared from Wisconsin about 1840 (Hay, 1882) and probably from the Upper Peninsula of Michigan about the same time.

Native woodland caribou remained in the Red Lake Wildlife Refuge of northwestern Minnesota until about 1940 when the last one was found crippled and dying. However, in 1938, ten caribou were live-trapped near Montreal Lake, north-central Saskatchewan, and reintroduced to the Refuge. Eight of these animals were calves and were kept in an enclosure

until 1942 when they and their progeny numbering 15 to 20 animals were released (Swanson, Surber, and Roberts, 1945). They were noted until 1943. However, none were observed in an aerial survey of the Refuge conducted in 1946 (Nelson, 1947). Cringan (op. cit., p. 487) reported a sight record near Manitou Rapids, Minnesota, during the winter of 1954-55.

Malaher (in Cringan, op. cit.) reported that after reaching a population low point in Manitoba between 1930 and 1950, woodland caribou were increasing and might total 4,000 or more. They are believed to still occur in small numbers scattered through northern Saskatchewan. A few scattered groups still remain in the Montreal Lake area from where the Minnesota transplant was taken (Banfield, 1951). Stelfox (in Cringan, op. cit.) estimated between 700 and 1,000 woodland caribou in Alberta and thought that the population was fairly constant.

The present status of caribou in the Pacific Northwestern States has been the subject of an extensive investigation by Evans (1960). Flinn (1959) reported that approximately 100 caribou still survived on winter ranges in northern Idaho in the Salmo River region. Riis (1938) presented recent records for Washington State (two killed near Salmo River, 1936) and Montana (Yaak River, 1934, and upper Flathead River, 1935).

There are no recent estimates of populations of this caribou form in British Columbia, southern Yukon Territory, or Mackenzie District, N.W.T. Woodland caribou are still to be found in the Kluane Game Sanctuary and in small bands in a few other southern Yukon localities (Banfield, 1961). In southeastern Alaska, this form is extinct in the Kenai Peninsula, but small numbers are still reported from the Copper River area. Scott, Chatelaine, and Elkins (1950) estimate the population at about 150 animals.

If guesses are made for the populations of caribou in British Columbia (5,000), Saskatchewan (2,000), Yukon (1,000), Mackenzie District (3,000), then the present total population of woodland caribou would be about 43,000 animals.

Taxonomic History

The type locality of Gmelin's *caribou*, usually quoted as "Eastern Canada," should be restricted to a definite locality. Following Thomas's (1911) advice, I have used the "primary reference" method. Gmelin's primary reference is Brisson (1762) which has been rejected by the International Commission on zoological nomenclature. The second reference is to De Charlevoix (1744). In that work (op. cit., 5: 191) there is a lively description of a caribou, while fleeing from hunters at Quebec, crossing the frozen St. Lawrence River, only to fall into the hands of a band of Canadians camped on the south shore at Lévis. The incident was reported to have occurred a few years before 1721. Gmelin's third reference is to Dobbs (1744), who only repeated Jérémie's earlier (1720) account of caribou between the Churchill and Nelson rivers, northern Manitoba. Unfortunately, it is difficult to decide whether that reference refers to *groenlandicus* or *caribou*, and there is the additional problem of Richardson's *sylvestris* then being synonymous with Gmelin's *caribou*. The type locality for *caribou* is hereby restricted to Quebec City, based upon Gmelin's second reference to De Charlevoix. Unfortunately, the subspecies is now extirpated from the immediate vicinity of Quebec City, but specimens are available from Laurentides Provincial Park, about 60 miles to the north.

Richardson's *sylvestris* clearly referred to the woodland caribou. It has been found that woodland caribou from northern Manitoba do not differ from eastern specimens (Tables 18 and 19).

Audubon and Bachman (1856) re-applied the name *caribou*, with some hesitancy, to the reindeer of North America. They wrote (op. cit., p. 111): "According to our opinion two species of this genus exist—one in the Old World (*Rangifer tarandus*) commonly called the Lapland Reindeer, and the caribou (*Rangifer caribou*) and its varieties, the reindeer of the American continent. Should, however, the varieties of the Reindeer found in different parts of the Arctic Circle on both continents form one species only, then there is but one species of the genus known at present."

They then clearly described the woodland caribou of New England, Quebec, and the Maritime Provinces, remarking that the polar forms might be found to be *tarandus*.

The naming of the Newfoundland population of caribou involved one of the most flagrant breaches of professional ethics known in mammalogy (today it might pass as "gamesmanship"). In Boston on November 10, 1896, Allen is reported to have shown Bangs his manuscript, which was in press, describing *R. terraenovae*. That evening Bangs secretly redescribed the form using the same name but inserting another type specimen from his Institute's collection. The following day he had his one page leaflet printed (Bangs, 1896) in Boston and passed out copies to Allen and others that evening. The leaflet bears the notation "Wednesday, November 11, 1896, 5 p.m." Allen's (1896) description was published on November 21, 1896, in New York.

After crossing the broad prairies, devoid of satisfactory caribou habitat, the early explorers to western North America found large, dark, heavily antlered caribou in the Cordilleran region which they referred to as mountain caribou (Hamilton Smith, 1827). Seton (1899) described the mountain form, comparing it to Bangs *terraenovae*. He mentioned that it was "Separated geographically from woodland caribou by a vast caribou-less basin up the east slope of the Rockies to 54°."

However, it was suspected by naturalists who were familiar with both populations in the field, that the mountain caribou of the southern Rocky Mountains was the same form as the woodland caribou, since the caribou range was continuous across the continent in the boreal forest region north of the prairies. The assignment of Seton's *montanus* and Hollister's *fortidens* to the barren-ground *arcticus* group by Jacobi has always seemed an anomaly.

It is just as surprising that J. A. Allen's names, *stonei* and *osborni*, were accepted in the literature for so long a time without a serious challenge. Unfortunately, the type specimen of *stonei* was one of the last caribou taken on the Kenai Peninsula. Since that period the local population has been extirpated. Elliot (1901) described and illustrated two other specimens of caribou from the Kenai Peninsula in a private collection in Chicago and discussed the validity of Allen's *stonei*. He wrote (op. cit., p. 61): "Failing then to distinguish the Kenai Peninsula caribou as a distinct form by any of the characters mentioned by Dr. Allen, apparently nothing remains but the color." He then proceeded to describe the wide range in colour in the limited specimens at hand and finally concluded: "It is very evident that

our knowledge of western and northwestern caribou is very imperfect and unsatisfactory, our material being altogether insufficient, and while it is the easiest thing in the world to describe specimens as 'distinct,' it is best to make haste slowly until ample evidence is obtained to establish a fact."

One of the antlers figured by Elliot (pl. 12) from the Kenai Peninsula is typically a woodland caribou in general conformation.

Osgood (1909) was the next taxonomist to study the caribou complex in northwestern America. He identified caribou specimens from Eagle and Circle, Eastern Alaska, as *stonei*, based upon antler formation. He then wrote (op. cit., p. 17): "They appear to be intermediate in character as well as in range between *stonei* and specimens from east of the Yukon referred to as *arcticus*. Therefore, *stonei* is treated as a subspecies of *arcticus*. That *stonei* may intergrade to the southward with the so-called woodland form *osborni* is very probable, as caribou are known to inhabit practically all suitable parts of the country intervening between localities from which the two forms are now known. Moreover, the differences between the two are all relative, excessively variable, and rather intangible."

In the same publication, Osgood (op. cit., p. 50) identified specimens from Coal Creek, Ogilvy Mountains, central Yukon Territory, as *R. arcticus*. He also mentioned that specimens from northwest of Rampart House, northern Yukon Territory, were referable to *arcticus*. He noted that the legs of the Ogilvy Mountain specimens lacked the more extensive white stripes of typical *arcticus*.

Concerning the caribou of the Macmillan River region of eastern Yukon Territory, Osgood (op. cit., p. 76) wrote: "The caribou of the Macmillan region are referable to *R. m. osborni*, a member of the so-called Woodland Group. Yet in habits and in nearly all respects save size, they seem scarcely to differ from the caribou of the Ogilvy Mountains (see p. 49), which are distinctly referable to the Barren-Ground Group . . . It is, therefore, difficult to believe that a sharp line exists separating *osborni* from *arcticus* . . . but it seems probable that our northwestern caribou, like the sheep, will eventually prove to intergrade, so that forms now known as species will rank only as subspecies."

Osgood also remarked on the general tendency to long, rangy antler beams in the Macmillan region "which may be in the nature of a gradation towards *arcticus*." None of the antlers were reported to be short and flattened as is typical of *montanus* "and is found also in certain specimens of *R. m. osborni* from the type locality."

Murie (1935) was the next author to attempt an analysis of the caribou populations of Northwestern America. He concluded (op. cit., p. 82) that differences between *stonei* and *osborni* were "surprisingly small." In pelage, he commented, "the two groups are essentially the same." The antlers showed "similar variations and general characters." The one distinct difference he noted was in the length of the tooth row. The tooth rows of 21 *osborni* averaged much longer than the tooth rows of 22 *stonei*. However, he chose the Yukon-Tanana herd of caribou from central Alaska as typical of *stonei*, while he had only the type of *stonei* from the Kenai Peninsula in the series of 22 animals. The larger series of animals from Alaska, studied in the present investigation, have clearly shown a cline in most measurements, from large in southern Alaska to small in northern Alaska. It is therefore not

surprising that a series predominantly from central Alaska would average shorter than a series from northern British Columbia. The important fact is that the one specimen from the Kenai is indistinguishable from the British Columbia specimens. Murie concluded (op. cit., p. 83): "it seems logical to consider *osborni* as an intermediate form between the stocky antlered woodland caribou to the southeast and the more 'rangy antlered' representatives of the barren-ground caribou to the north."

From this rather detailed review, it is evident that there were many precedents for the present opinion that Allen's *osborni* was synonymous with his previous *stonei* and that, actually, both forms were intergrades between woodland and barren-ground caribou in northwestern America, as described in the present account.

Hollister (1912a and b) described *fortidens* from the headwaters of the Smoky River in the Alberta Rocky Mountains as being the largest and darkest caribou. He also mentioned that the females were normally antlerless. Specimens from that area are indistinguishable from Seton's *montanus*, or western woodland caribou. Holsworth collected a series of mountain caribou from the Pine River area of the Rocky Mountains, B.C., approximately 100 miles to the north, which were deposited in the U.S. National Museum. Holsworth (1930, p. 408) reported on the study of those specimens, as follows: "Much to the surprise of Dr. Preble of the United States Biological Survey, who undertook to study and classify them, they proved to resemble closely the eastern type of woodland caribou. He wrote to me as follows about them: 'The caribou have proven to be very interesting in that they represent the eastern woodland type of caribou and not the one that is found in the mountainous regions of British Columbia'."

Mr. T. D. Carter of the American Museum of Natural History commented upon two specimens from Thorval Creek, Alberta, in Crowe (1943): "although these caribou were taken within sight of Mt. Robson, the type locality of *fortidens*, they agree more closely with *montanus* in their dental characters."

Dr. G. M. Allen described *caboti* from Nachvak Fiord, Labrador, as a subspecies of the barren-ground caribou *arcticus*, based upon a single shed antler. The next year an adult male specimen, MCZ 24890, was received but was never described. Curiously, a large series of 17 adult skulls had been obtained for the U.S. National Museum from Fort Chimo, Quebec, in 1884, by the anthropologist L. M. Turner, but they had not been studied until the present investigation. The herds that inhabited the central Ungava region of Quebec and Labrador may be characterized by being greyer than the typical woodland caribou. The males predominantly carry great heavy antlers.

Millais (1915) described a number of local American varieties of reindeer without picking type specimens or sometimes without restricting the type locality. The names: *keewatinensis*, *labradorensis*, and *ogilvyensis* have been generally considered synonyms of earlier named forms. *Labradorensis* might well have been the name for the Ungava form, if G. M. Allen had not described it the year before. *Keewatinensis* seems to be a synonym of *sylvestris*, and *ogilvyensis* the name of a hybrid population between *caribou* and *groenlandicus*, as previously described in the section dealing with Allen's *stonei* and *osborni*.

Figgins's (1919) *mcquirei* from southwestern Yukon was considered indistinguishable from *stonei* and *osborni* by Murie (1935), and the present study has confirmed that analysis.

Barclay (1935) has the distinction of proposing the latest name to an already crowded roster of American caribou names for the population from the south fork of the Macmillan River, Yukon Territory. He described a large caribou, generally paler than *montanus*, possessing large antlers with long tines "not bifurcate as in *osborni*." More specimens from the general area have indicated that the local population constitutes another step in the general cline between *caribou* and *groenlandicus*, previously discussed by Osgood (1909). Barclay, in an appendix to Armstrong (1937), assigned a broader range to his form in eastern Yukon.

Remarks

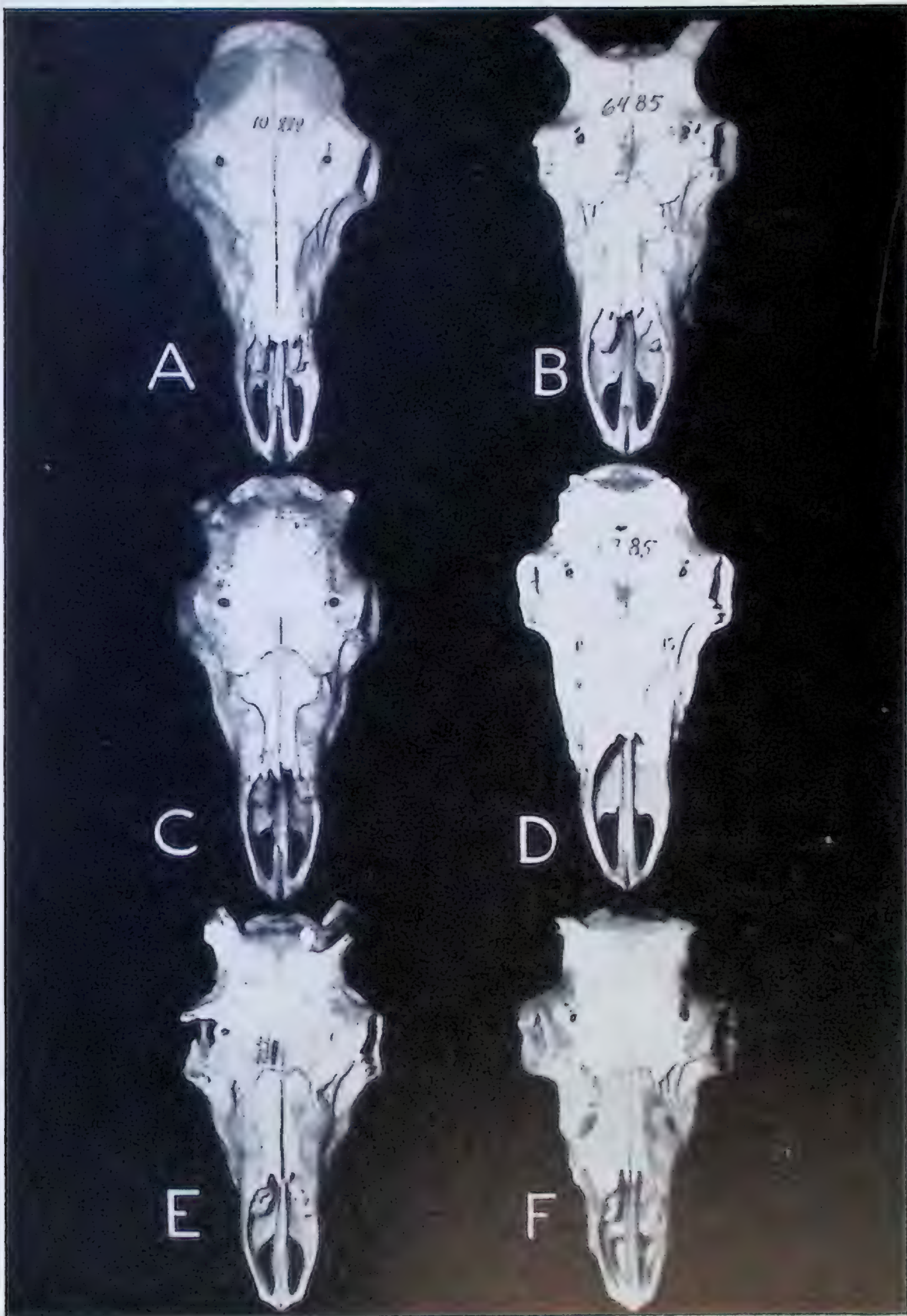
One would not expect the woodland caribou to be identical across their vast range. As a group, the herds show certain common characteristics, statistically significant, which set them aside from the tundra reindeer. Yet, on both extremities of their range in northwestern Ungava and in Alaska, Yukon Territory, and the Mackenzie Delta region, intergradation in these characters occurs in adjacent herds. Elsewhere, particularly in the central Mackenzie District and the northern Prairie Provinces, the two forms often occur sympatrically and behave as though there were isolating factors that distinguished the forms on a species level.

On the other hand, several populations within the forest range of the woodland caribou show some constant features. However, the total effect of this variation is a mosaic pattern. Some factors indicate clines in one direction, whereas other factors have opposite clines. Sometimes the variation pattern is different for the sexes. Several of these populations had been given taxonomic names, and their characters were analysed statistically in a preliminary phase of this study (See Tables 18 and 19). Since, statistically, significant relationships did not appear, the forms are not considered to represent valid geographic subspecies. The variation illustrated is believed to be on a deme level below the recognized trinomial level.

However, since infraspecific evolution is a dynamic affair, these demes may eventually achieve subspecific rank if extinction is not their fate. Therefore, some of their characteristics are described in more detail in the present section.

The Newfoundland caribou was one of the first populations accessible at all seasons and, therefore, one of the first to receive a scientific name. They are of average size with a heavy build and a shortened neck.

The colour is usually brown but quite variable (Dugmore, 1913). In the autumn the flank stripe is, as a rule, rather vague: paler eye rings are frequently present; the socks are usually wide with a light stripe extending up the back of the legs. About the only fairly constant marks are a very dark chocolate face and a light flash on the back of the thigh. An adult male (BMNH 8-1-19-1) in fresh autumn pelage may be described as follows: muzzle, Light Buff; face, Prouts Brown; neck, Cartridge Buff; back, Snuff Brown; flank stripe, Light Buff; chest, Snuff Brown; belly, Tilleul Buff; legs, Prouts Brown (Tilleul Buff behind); wide socks. An adult female (BMNH 8-1-19-2) in similar pelage may be described as



Dorsal views of reindeer skulls, primarily Old World subspecies: (A) *fennicus*, male; (B) *fennicus*, female; (C) *tarandus*, male; (D) *tarandus*, female (Novaya Zemlya); (E) *eogroenlandicus*, male; (F) *platyrhynchus*, male (Scale = $\frac{1}{2}$ ca.).

follows: muzzle, Tilleul Buff; face, Snuff Brown; neck, Pale Pinkish Buff; back, Bister; flank stripe, Pale Pinkish Buff; chest, white; belly, white; legs, Snuff Brown; socks, wide.

In winter, Newfoundland caribou were described as uniquely white. That was at a time when few caribou populations came under observation during the winter. Now it is known that many caribou populations in northern Quebec, Labrador, Ontario, Northwest Territories, and elsewhere become very pale in late winter as a result of changes in hair colour through growth, fading, and breakage. It is no longer possible to differentiate the Newfoundland caribou from the Quebec caribou on that ground.

The normal antler formations of Newfoundland caribou are short, heavy, and broadly palmate. The tines are numerous but generally short. There are more rangy antlers, found generally on older bulls. Up to 42 per cent of normal females are antlerless (Millais, 1907). The skull characteristics will be discussed later.

The caribou of Labrador and Quebec were also given a scientific name. Originally Allen outlined the distribution of his form as extending south to the Strait of Belle Isle and meeting the range of woodland caribou "in the interior." Later authors (i.e. Anderson, 1938) have drawn a sharp dividing line across the peninsula from the Hamilton Inlet to the foot of James Bay and allocated the northern range to the Ungava caribou and the southern portion to woodland caribou. There has been no taxonomic study of the local situation prior to the present study. As one would expect, there is no dividing line between the two forms, because there are no geographic or historical barriers in the area. The woodland caribou throughout the whole peninsula are essentially similar from the Gulf of St. Lawrence to Fort Chimo. There are intergrading characteristics which become more prominent in northwestern Ungava between tundra and forest caribou. Unfortunately, however, the caribou in that area have been decimated by excessive hunting and destruction of their range by forest fires (Banfield and Tener, 1958) until only small numbers remain. The specimens available are inadequate to give a fair appraisal of the situation.

The Ungava caribou are generally large (as indicated by Millais, 1915, but not by G. M. Allen, 1914). They appear to be longer-limbed and longer-necked than the Newfoundland caribou, but these characters may not be significant. The general colour tone in autumn is more grey-brown than is normal in woodland caribou. An adult male (NMC 21743) in autumn pelage may be described as follows: muzzle, silvery; face, Clove Brown; neck, Tilleul Buff; back, Avellaneous; flank stripe, Tilleul Buff (vague); chest, Hair Brown; belly, white; legs, Olive Brown; socks, wide, white. An adult female in autumn (NMC 49-16) may be described as follows: muzzle, silvery; face, Fuscous Black; neck, Tilleul Buff; back, Warm Sepia; flank stripe, Tilleul Buff; chest, Hair Brown; belly, white; legs, Clove Brown; socks, wide, white.

The normal antlers carried by adult males are their most characteristic feature. The beams are extremely long, round, and broadly sweeping; the terminal tines are frequently carried forward by the long arc of the beams. The brow and bez tines are broadly palmate as are the terminal portions occasionally; posterior tines are often lacking. This was the diagnostic feature of the named variety. However, variations are to be found, and

short, heavy flattened beams which are typical may be found particularly in southern Labrador. Antlerless females are again commonly observed. Jacobi (1931) mentioned the resemblance of these antlers to European prehistoric reindeer.

The typical woodland caribou of the Maritimes, New England States, and southern Quebec is fairly constant in form. The animals are of medium size with long limbs. The coloration is generally dark brown; flank stripes are restricted, and bellies are dark. The palmate antlers are usually longer than those in the Newfoundland herds but with weaker terminal tine formation. Beams are frequently ridged.

The woodland caribou of western Ontario, the Prairie Provinces, the Mackenzie District, and the southern Rocky Mountains are quite uniform over a vast range. They are larger than the Newfoundland and Eastern forms but with the same general colour and antler formation.

The taxonomic status of the caribou herds that formerly inhabited the southern Hudson Bay coast from Cape Henrietta Maria, Ontario, to Cape Churchill, Manitoba, has remained a puzzle. When Europeans first established fur-trading posts at the mouths of the Nelson and Hayes rivers, Manitoba (York Factory and Fort Bourbon), at the beginning of the eighteenth century, they encountered herds of migratory caribou which spent the winters in the wooded interior of Manitoba and migrated south-eastward to the narrow tundra strip along the Hudson Bay coast (Jérémie, 1720; Hearne, 1795). Through the co-operation of officers of the Hudson's Bay Company, I was privileged to examine the caribou references in the records of York Factory and Churchill River (Fort Churchill, Man.) posts during the period 1714 to 1726. Those records confirm Jérémie's reports of caribou migrations in the area. Unfortunately, as a result of the heavy kill of migrating caribou in pounds and snares, in order to provide provisions for the establishments and their native visitors, these herds were rapidly reduced in the eighteenth century and soon forsook routes in the vicinity of the post. However, a few migratory bands still inhabited the tundra west of the Severn River, Ontario, as late as 1912 (Tyrrell, 1913).

Whether those herds were migratory woodland caribou or the southernmost herd of tundra caribou is uncertain. Preble (1902) considered them to be woodland caribou. Unfortunately, those herds were decimated or exterminated before specimens were secured. Through the co-operation of the Manitoba Game Branch, I have examined specimens from current populations in the Shamattawa and Hayes River area that appear to be woodland caribou, which undertake no pronounced migrations. Resident caribou are still reported from the Owl River area north of York Factory. Unfortunately, when the area was examined in 1949 it was overrun by migrating tundra reindeer (Banfield, 1954b). It is possible that this was another area of intergradation between the subspecies. Reduction of the local populations has apparently curtailed the migratory habit.

The mountain caribou of the Cordilleran region of northern British Columbia and southern Yukon Territory appear to be another deme. They are probably among the largest groups (The largest specimen of woodland caribou came from Great Bear Lake, N.W.T.). An adult male (NMC 2264) in autumn pelage may be described as follows: muzzle, Ivory Yellow; nose, Fuscous Black; cheeks, Fuscous; neck, Cartridge Buff to Tilleul Buff; back,

Clove Brown; flank stripe, Tilleul Buff; chest, Bister; belly, Tilleul Buff (restricted); legs, Bister; socks, narrow. An adult female (NMC 2259) in similar coat was as follows: muzzle, silvery; face, Fuscous; neck, Drab Gray; back, Clove Brown; flank stripe, Drab Gray (restricted); chest, Clove Brown; belly, Hair Brown; legs, Bister; socks, white (narrow). The neck and flank stripe of mature bulls are frequently creamy coloured. Prominent eye rings may be present on some animals.

The antler formation of this group is highly variable. Some antlers are typically short, heavy, and palmate. However, many are more rangy with fairly long beams and long digitate terminal tines. The length of the tines is one of the features of this group. It is believed that this character is an expression of intergradation between the forest type and the long digitate tundra type of antlers.

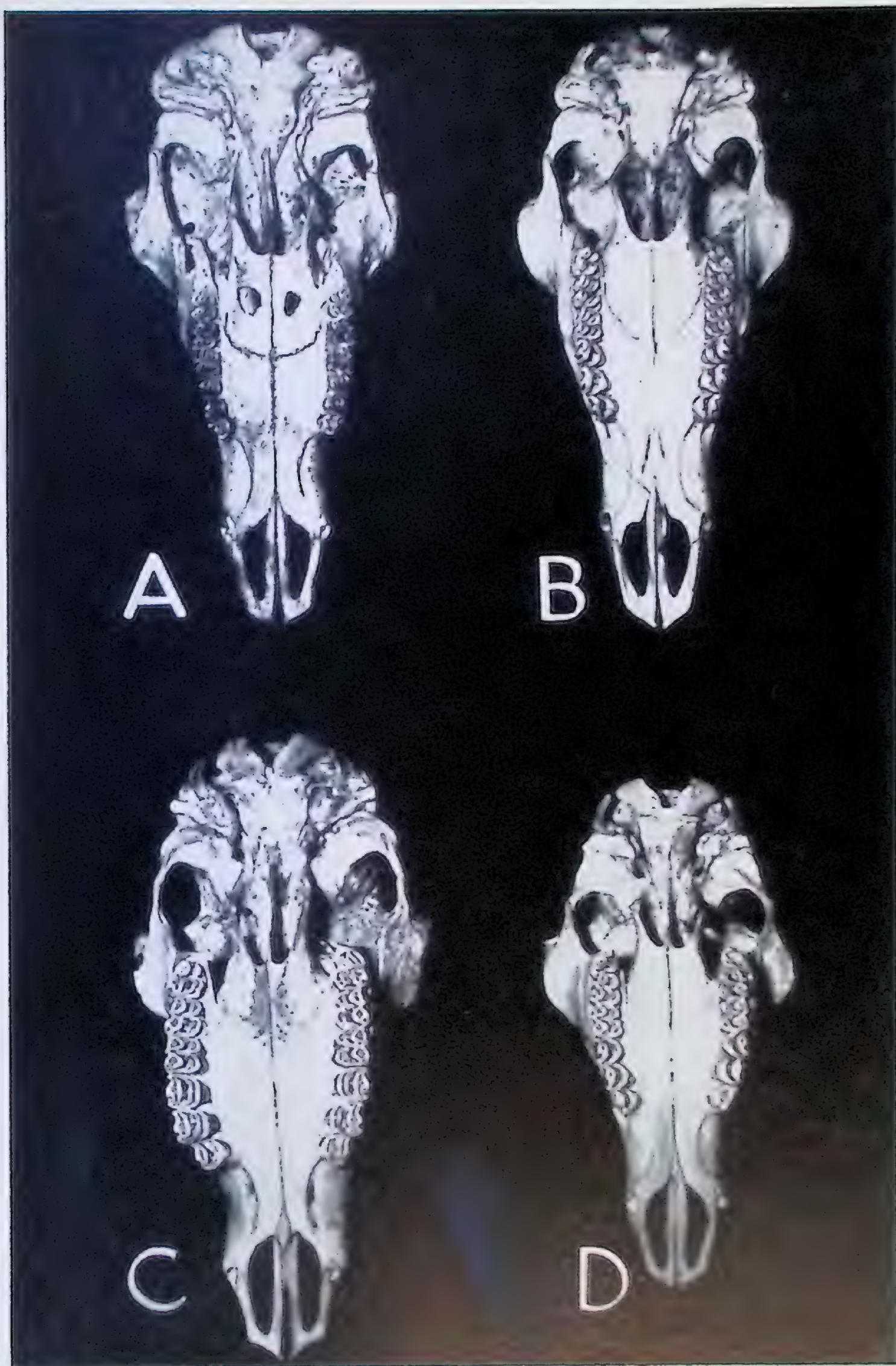
In east-central Yukon Territory the woodland characteristics become less prominent. The local caribou are smaller, greyer, with more white on flanks, bellies, and backs of legs. The antlers are more slender and digitate. Many long tines again occur quite commonly.

It is in the analysis of variations of the skulls of those groups that the full effect of the mosaic pattern of variation is appreciated (Tables 18 and 19). In the basal length of males, the Ungava, western woodland, and northwestern forms are large, as opposed to Newfoundland and eastern forms, but in females the northwestern group was smaller than the eastern group. In orbital width, most male groups are about the same, except the eastern males, which are narrower. There is a west to east cline among females, with the Newfoundland group ones narrowest. In nasal length, the eastern groups are similar and longer than the western groups of both sexes. In tooth row, western males and females were larger than eastern groups. In diastema, the Ungava male group was longest, followed by the western, the Newfoundland, and the eastern group which is the smallest. In females there was a similar cline, except for the Newfoundland females, which were the smallest. In occipital height, northwestern, western, and eastern males were similar, as opposed to lower occiputs in Ungava and Newfoundland forms, but among females there was a gradual cline from higher occiputs in the northwest to lower in the east.

It appears that the various populations of forest caribou share a common genetic pool of characters that in total make them recognizable as caribou. Yet, certain characteristics have become phenotypically dominant in certain demes, although they may occur rarely elsewhere. Other characters, such as paler pelage, antler velvet, and digitate antlers, are possessed by widely separated demes on the extremities of the range. Those are thought to be phenotypic expressions of genetic factors introduced from nearby populations of tundra reindeer.

Specimens Examined

A total of 256 from the following localities: NEWFOUNDLAND: Grand Lake, 1 (AMNH); Badger, 2 (CM); Grand Falls, 1 (NMC); Sandy Lake, 1 (NMC); Victoria Lake, 3 (NMC); Louse Lake, 2 (NMC); Middle Ridge, 1 (NMC), 1 (ROM); Carmack, 1 (ROM); St. George, 2 (MCZ); Codroy, 2 (MCZ); no locality, 5 (AMNH), 1 (ROM), 1 (UKM), 2 (BM(NH)), 5 (NMC), 2 (MCZ). NOVA SCOTIA: Victoria Co., 2 (NMC);



Ventral views of skulls primarily Old World subspecies: (A) *fennicus*, male; (B) *tarandus*, female; (C) *platyrhynchus*, female; (D) *cogroenlandicus*, male (Scale = $\frac{1}{4}$ ca.).

no locality, 1 (USN). NEW BRUNSWICK: Tobique River, 1 (AMNH); Miramichi River, 2 (MCZ); Nipisiquit River, 1 (MCZ), 1 (USN); Nicatau, 1 (USN); Chipman, 1 (USN); Bathurst, 1 (USN); Newcastle, 1 (USN); no locality, 1 (AMNH), 1 (MCZ). MAINE: "Waddy Brook" (Wadleigh Stream, Piscataquis Co.), 1 (AMNH); Aroostook Co., 1 (AMNH); Lake Umbagog, 1 (MCZ); Upton, 1 (MCZ); Calais, 2 (UKM); Houlton, 1 (USN); no locality, 1 (MCZ). QUEBEC: Mont Albert, 1 (AMNH), 1 (ROM), 7 (NMC); Gaspé, 1 (NMC), 1 (QDG); Lake Temiscouata, 1 (USN); St. Raymond, 1 (USN); Lac Edouard, 1 (USN); Laurentides Prov. Park, 2 (BM(NH)); Baie Comeau, 3 (QDG); Vermilion River, 1 (CM); Seal Lakes, 3 (CM); Saguenay District, 1 (MCZ); Payne Lake, 2 (NMC); Leaf River, 2 (NMC); Diana Bay, 1 (NMC); George River, 2 (NMC), 2 (RM); Knob Lake, 1 (NMC); Fort Chimo, 17 (USN); Indian House Lake, 1 (AMNH). LABRADOR: Hebron, 1 (MCZ); Nachvak Fiord, 1 (MCZ); Straits of Belle Isle, 3 (MCZ); Port Hope, 3 (NMC); Mealy Mts., 2 (NMC); Red Wine River, 5 (NMC); Paradise River, 1 (USN); Capelin Bay, 2 (USN). ONTARIO: Slate Islands, 3 (ROM); Sioux Lookout, 1 (ROM); Hammell Lake, Patricia Dist., 1 (ROM). MANITOBA: Kaska, 2 (MGB); Shamattawa, 1 (MGB); Cranberry Portage, 1 (MGB); Wabowden, 2 (MGB); York Factory, 4 (MGB); Hole Lake, 1 (NMC); Limestone Bay, Lake Winnipeg, 1 (NMC); Lac du Bonnet, 1 (NMC); Nelson River, 1 (USN); The Pas, 1 (UBC); no locality, 1 (USN). MINNESOTA: Lake of the Woods, 5 (UKM); Red Lake, 1 (USN). SASKATCHEWAN: Meadow Lake, 1 (NMC). ALBERTA: Thorval Creek, 2 (AMNH); Jasper National Park, 1 (AMNH), 7 (UBC), 2 (NMC); Sheep Creek, 1 (CM); Entrance, 3 (UA); Porcupine Lake, 1 (USN); Fort McMurray, 1 (USN); Smoky River, 1 (USN); Jackfish Lake, Wood Buffalo Park, 2 (NMC). BRITISH COLUMBIA: Trimble Lake, 1 (AMNH); Leval Mts., 2 (AMNH); Gold Range, 3 (AMNH); Golden, 1 (AMNH); Kootenay Landing, 1 (BCGC); Creston, 1 (BCGC); Wells Gray Park, 2 (BCP); Ominica Mts., 1 (BCPM); Vernon, 1 (BCPM); Selkirk Mts., 2 (UBC); Okanagan Lake, 1 (BM(NH)); Glacier National Park, 1 (NMC); Sheep Creek, 1 (USN); Wapiti River, 1 (USN); Pine River, 2 (USN); Jarvis Pass, 1 (USN); Bull Moose Creek, 1 (USN); Cassiar Mts., 4 (AMNH), 1 (CM), 1 (NRM), 1 (USN); Telegraph Creek, 1 (BCPM); Dease Lake, 2 (CM), 1 (USN); Eagle River, 1 (USN); Markill River, 1 (CM); Skeena River, 1 (NMC); Big Salmo, 2 (USN). WASHINGTON: Salmo Mt., 3 (USN); Okanogan Co., 1 (USN). NORTHWEST TERRITORIES: Fort Simpson, 2 (NMC); Fort Reliance, 1 (NMC); South Nahanni Valley, 2 (NMC); Keith Bay, Great Bear Lake, 1 (NMC); Fort Rae, 1 (USN). YUKON TERRITORY: Teslin Lake, 18 (NMC); Rose River, 1 (NMC); Hootalinqua River, 1 (NMC), 1 (USN); Wolf Lake, 1 (NMC); Stoneaxe Lake, 2 (NMC); Macmillan River, 1 (BM(NH)); Pelly River, 1 (USN); White River, 2 (USN). ALASKA: Kenai Peninsula, 1 (AMNH); White River, 2 (AMNH); Kodiak, 1 (UKM).

Rangifer tarandus dawsoni Seton

Queen Charlotte Island Caribou

- 1900. *Rangifer dawsoni* Seton-Thompson, Ottawa Nat., 13(11): 257-261.
- 1915. *Tarandus rangifer dawsoni* (Merriam), Millais, The gun at home and abroad, 4: 269.
- 1915. *Rangifer tarandus dawsoni*, Lydekker, Cat. Ungulate Mamm. in the British Mus. (Nat. Hist.), 4: 251.

1931. *Rangifer arcticus dawsoni*, Jacobi, Das Rentier, Akad. Verslag., p. 95, Leipzig.
 1952. *Rangifer tarandus dawsoni*, Flerov, Fauna USSR, vol. 1, no. 2, Musk deer and deer, p. 247.
 1956. *Rangifer dawsoni*, Cowan and Guiguet, The mammals of British Columbia. B.C. Prov. Mus. Handbook, 11: 383.
 1959. *Rangifer tarandus dawsoni*, Hall and Kelson, The Mammals of North America, 2: 1018. Ronald Co., New York.

Holotype. Cranium and right antler of a male, British Columbia Provincial Museum, No. 1483, Victoria. Collected by Alexander Mackenzie in 1882 (?).

Type locality. Foothills west of Virago Sound, north end of Graham Island, Queen Charlotte Islands, British Columbia.

Diagnosis. A small mouse-coloured caribou, darker on face and lighter on neck, belly, and legs; no prominent flank stripe. Antlers brown, small, and remarkably irregular; brow and bez tines digitate; few other tines.

Biology. Very little is known of the biology of this form. They occurred in small groups and probably undertook local seasonal migrations. The antlers of bulls were irregular, and the females were usually antlerless (Cowan and Guiget, 1956).

Habitat. Treeless bogs in humid boreal forest.

Description

There are no complete skulls in existence, and the specimens have deteriorated since they were examined by Merriam in 1911 (Merriam in Sheldon, 1912, Appendix C).

Average Skull Measurements

Some of Merriam's measurements of specimen BCPM 1486 are therefore repeated here for comparison. Estimated maximum length of skull, 350; orbital width, 156; nasal length, 105; nasal breadth, 52; diastema, 98; tooth row, 88; mandible (from personal measurements) length, 252; tooth row, 95; diastema, 84.8; mandibular height, 114. Merriam also reported the maxillary tooth row of a young female as 93 and the mandibular tooth row as 100. I obtained the following measurements from the type cranium: orbital width, 149; mastoid width, 124.

External Measurements

Antlers of males: length (of type), 730; length and spread of No. 1,486, 930, and 730 respectively; antler vertical diameter, 39 to 42; antler horizontal diameter, 25 to 31.

Mature male (BCPM 1484): total length, 1,910; tail, 110; hind foot, 385; shoulder height, 1,050; mature female (BCPM 1487): total length, 1,550.

Pelage

In November: adult female (BCPM 1487): back, Fawn Color; neck, eye ring, belly, and legs, Vinaceous Buff. There may have been considerable fading during storage. The mounted specimen is much faded.

Distribution

Known in life only from the plateau west of Virago Sound, Graham Island, Queen Charlotte Islands, B.C. Millais (1915, p. 269) reported a skull taken from a glacier at the mouth of the Skeena River on the coast of British Columbia.

Status

Probably extinct; last evidence about 1935.

Taxonomic History

The rarest and most restricted form of caribou was first reported by Dr. G. M. Dawson (1890), the founder of the National Museum of Canada. During geological investigations in the Queen Charlotte Islands in 1878 he obtained Indian reports of a native cervid and at first concluded that it was a wapiti (*Cervus elaphus roosevelti* Merriam). Later, he was shown the skin and skull of a local specimen by Mr. William Charles, an employee of the Hudson's Bay Company, and recognized them as a caribou's.

Dawson, in 1899, drew the attention of Ernest Thompson-Seton to his account and to the specimen. Seton (who used various combinations of his name on publications) examined the type specimen in the British Columbia Provincial Museum at Victoria and described the form for science in 1900.

So secretive were the animals that W. H. Osgood (1901), who made a special investigation of the Islands in 1900, could find no definite evidence of their existence and concluded that the type specimen was a hoax, that it had been collected elsewhere on the mainland, and that caribou did not exist on the Islands.

However, additional evidence from the Haida Indians and the collection of a shed antler by Commander Hunt and Lieut. Bills on February 22, 1906 (1906), confirmed the existence of the Queen Charlotte Island caribou. Sheldon (op. cit.) spent a month in the area surrounding Virago Sound, from October 26 to November 23, 1906, searching for the illusive caribou. Although he found an abundance of tracks and dung, he failed to catch a glimpse of the animals.

Two years later, on November 1, 1908, two natives were hunting in a large bog, three or four miles inland from Virago Sound, when they saw a small herd of two bulls, a cow, and a calf. The three adults were shot, and the skins and skulls sent to the Provincial Museum at Victoria. The smaller bull (No. 1484) was mounted and is still on exhibition.

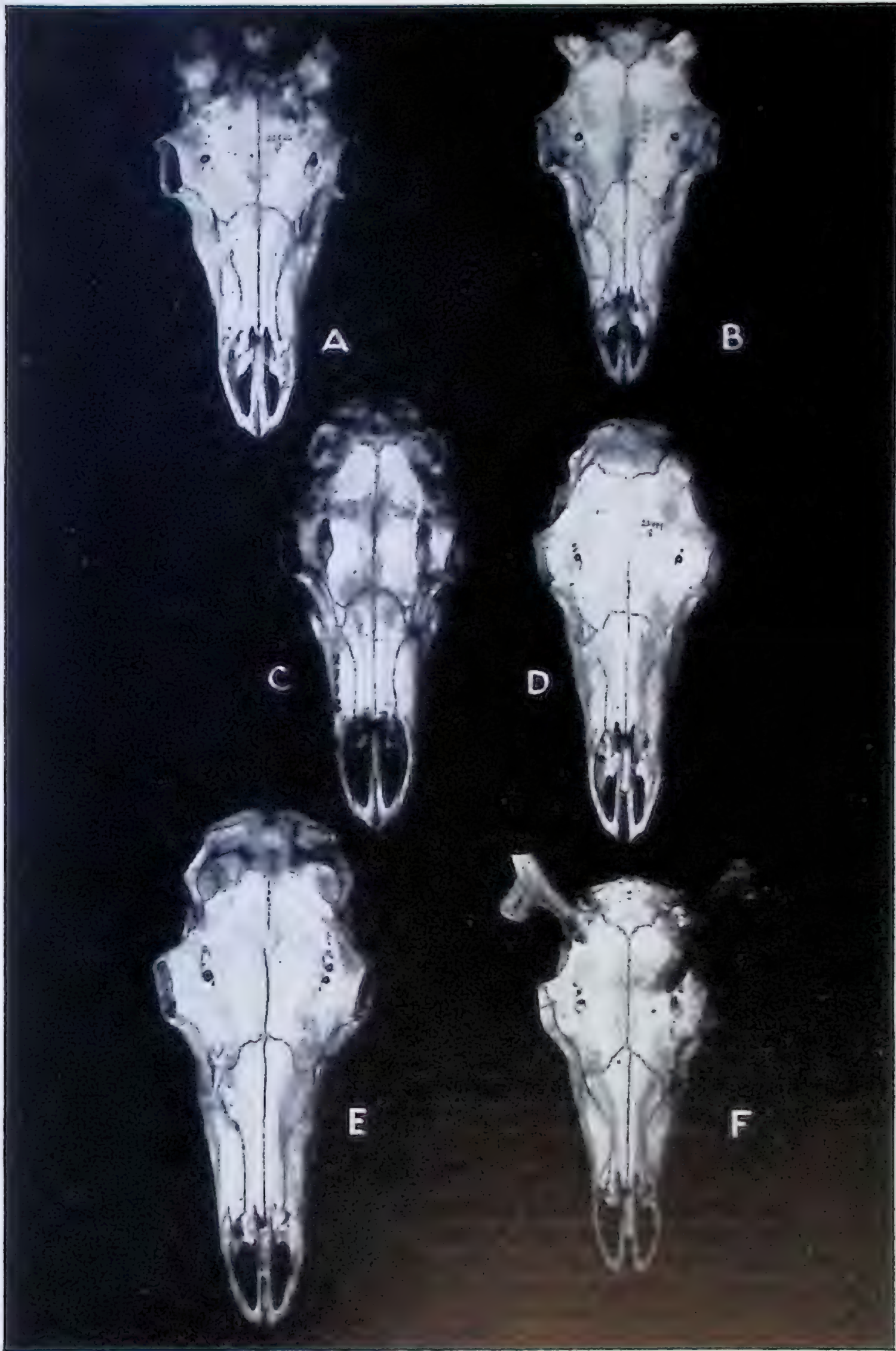
One of the hunters of the last group reported to Cowan (1936) that he had seen fresh caribou tracks the previous year. There has been no further evidence of the survival of this form.

Remarks

The Haida Indians of the Queen Charlotte Islands were primarily salmon fishermen. They hunted and trapped bear and otter, but those animals were taken along the water courses so that the Indians seldom penetrated the dense humid boreal forest. They seemed to have very little knowledge of the native caribou, and it is doubtful if they were a serious threat to its survival.

Although the history of the subspecies is scanty, a few conclusions may be drawn. In the first place the caribou were never plentiful. Although the type specimen was taken from a herd of unknown size in 1882, the three remaining specimens were taken from the only other group of four ever observed. The only other evidence reported were tracks, dung, and one shed antler.

Previous authors have remarked on the irregular antlers of the males. The mounted male specimen possesses very small antlers suggestive of a normal female. The females were said to be antlerless. This fact, coupled



Dorsal views of reindeer skulls of New World subspecies: (A) *pearyi*, male; (B) *pearyi*, female; (C) *groenlandicus*, male; (D) *groenlandicus*, female; (E) *caribou*, male; (F) *caribou*, female (Scale = $\frac{1}{3}$ ca.).

with its small size and restricted range, has led authors to suggest that it was a decadent race that succumbed naturally without human interference.

Dawson (1890) early pointed out that its existence on the Queen Charlotte Islands in the absence of wapiti and deer indicated an early occupancy of the Islands either when they were connected to the mainland by the Cordilleran Ice-Sheet filling Hecate Strait, or immediately afterwards when the Strait was dry, before the melting continental glaciers had raised the sea-level. In any event, it must be concluded that the offshore Islands provided caribou habitat in late Wisconsin times before more temperate ungulates such as wapiti and deer could reach them. Millais' (1915) record from a mainland glacier may indicate such a migration route. Heusser (1960) has confirmed the presence of a glacial refugium on the Queen Charlotte Islands during late Wisconsin times.

This population seems to be an outstanding example of the Sewell-Wright effect of genetic drift in an insular habitat. Cowan and Guiget (1956) considered the form to merit specific rank, pointing to its diagnostic features and complete isolation. However, it seems to me that the form possessed no unique features not found occasionally in other caribou populations. The diagnostic features were all relative and indicative of its isolated insular occurrence. Although isolated when discovered, it seems logical to suppose that it would be recognized as belonging to the same species if confronted by other caribou. It has been described as being very small, but the few measurements available suggest that it was similar in size to insular populations of tundra reindeer.

I have placed it in the woodland caribou series because of a combination of features: pelage, dull without prominent flank stripe; cranium, flat; eye sockets, not prominent; tooth row, long; and skull, generally narrow. In addition, the antlers, although irregular, are suggestive of some eastern woodland caribou in colour and in the possession of proximal posterior tines, weak terminal tines, as well as the antlerless condition of the females. Finally, the bog habitat is typical of woodland caribou. The woodland caribou of the Cordilleran region such as *R. t. fricki* of late Wisconsin deposits might be considered as ancestral.

Specimens Examined

A total of five from the Virago Sound area, Graham Island, Q.C.I., B.C., at BCPM. That Institution also has another set of antlers labelled as collected by J. Flemming in the Queen Charlotte Islands in 1876, but there is doubt in the accuracy of the data. These antlers are quite typically palmate of the woodland caribou.

Rangifer tarandus fennicus Lonnberg Eurasian Forest Reindeer

- 1909. *Rangifer tarandus fennicus* Lonnberg, Arkiv för Zool. Bd. 6, nr. 4: 10. July 14.
- 1912. *Rangifer fennicus*, Miller, Cat. Mamm. West. Europe, 981.
- 1912. *Rangifer phylarchus* Hollister, Smithson. Misc. Coll., 56(35): 6 (Kamchatka).
- 1915. *Tarandus rangifer chukchensis* Millais, The gun at home and abroad, 4: 220 (Domestic form, Kolimsk to Bering Strait).
- 1915. *Tarandus rangifer buskensis* Millais, The gun at home and abroad, 4: 222 (Sayanskiy Mts. near Tomsk and Busk Mts., near Semipalatinsk, Altai, USSR).
- 1915. *Tarandus rangifer yakutskensis* Millais, The gun at home and abroad, 4: 222 (Domestic form, Yakutsk, Amur and Transbaikal, USSR).

1931. *Rangifer fennicus*, *R. phylarchus*, Jacobi, Das Rentier, Akad. Verslag, Leipzig, pp. 125, 130.
1932. *Rangifer angustirostris* Flerov, Arbeit des Ausschusses zur Sci. USSR, Leningrad, p. 8. (Bargusin Mountains, Lake Baikal, USSR).
1933. *Rangifer tarandus valentinae* Flerov, J. Mamm., 14: 336 (Chulyshman River, Altai, USSR), and *R. t. phylarchus*.
1933. *Rangifer tarandus setoni* Flerov, J. Mamm., 14: 337 (Sakhalin Island).
1936. *Rangifer tarandus silvicola* Hilzheimer, Z. Sauget., 11(1): 155. (Olonetz, Karelskaya, ASSR.)
1936. *Rangifer tarandus transuralensis* Hilzheimer, Z. Sauget., 11(1): 155 (Konda River, Tyumen, USSR).
1936. *Rangifer tarandus dichotomus* Hilzheimer, Z. Sauget., 11(1): 157 (Seitowski Possad (?), near Orenburg, USSR).
1937. *Rangifer t. valentinae*, *R. t. phylarchus*, Sokolov, Soviet Reindeer Industry, vol. 9, 100 pages.
1951. *Rangifer t. phylarchus*, *R. t. angustirostris*, *R. t. valentinae*, *R. t. setoni*, Ellerman and Morrison-Scott, Checklist of Palaearctic and Indian Mamm., 1758-1946: 376.
1952. *Rangifer t. valentinae*, *R. t. phylarchus*, Flerov, Fauna of the USSR: Mammals, vol. 1, no. 2, Musk deer and deer, pp. 242-244.
1959. *Rangifer t. valentinae*, *R. t. phylarchus*, Sokolov (Fauna of the USSR): Mammals vol. 1, no. 3, Ungulates (Orders Perissodactyla and Artiodactyla), pp. 279-280.

Holotype. Skull of a male from Lapland, collected in 1854 by Prof. F. W. Mäklin, the University of Helsinki Zoology Museum, No. 809/1960.

Type locality. Torne District of Finnish Lapland (probably Enontekiö parish, northern Finland, Lonnberg, 1909).

Biology. Forest reindeer inhabit a variety of habitats across Eurasia from local alpine tundra to large bogs, but the choice of taiga predominates. Shaposhnikoff (1955) reported habitat choices and local altitudinal migrations in the Altai Mountains similar to those of the woodland caribou of mountainous regions of Canada. According to Sokolov (1959) the forest reindeer of the central taiga of Siberia migrate northward in summer toward the Arctic coast, particularly in the river valleys. Similar extensive migrations are also conducted by woodland caribou in the Labrador-Ungava region.

Shaposhnikoff reported the rut to commence about September 10 to 15 in the Altai Mountains, and the calves were born after the middle of May. He also reported the winter food in the taiga to include arboreal lichens and even mentioned the high percentage of antlerless females. In the museums visited I also observed antlerless female specimens from Karelia.

Description

See Tables 8 and 9 and Figures 8 to 15 for comparison of statistics of skull measurements between this subspecies and its neighbours.

Average Skull Measurements

Males: basal length, 359.8 (330-388); orbital width, 175.3 (164-189); nasal length, 121.6 (102-146); post nares, 44.08 (38.1-49.7); tooth row, 94.14 (84.5-103); diastema, 133.9 (122-149); occipital height, 153.7 (132-176).

Females: basal length, 321.6 (301-341); orbital width, 155.1 (143-165); nasal length, 112 (96-127); post nares, 38.33 (33.5-43.8); tooth row, 92.26 (85.2-99.0); diastema, 117.5 (105-126); occipital height, 130.6 (123-139).

External Measurements

There are very scanty data on the external measurements of this subspecies. One adult male was reported to have a total length of 2,200; shoulder height of 1,200 mm; length of hooves, 110 (95-135, $n=3$); width of hooves, 95 (90-100, $n=3$). (A summer male from Kamchatka (LIZ 24457) had amazingly small hooves measuring 74 in length and 65 in width.) Antler length, 847 (590-1,100, $n=8$); antler spread, 720 (450-1,100, $n=6$); beam vertical diameter, 46.2 (35-66, $n=7$); beam horizontal diameter, 31.7 (27-36, $n=7$). No measurements of females are available. Length of male metatarsus, 285; metacarpus, 208.

Pelage

The fresh autumn pelage of an adult bull (LIZ 36717, Karelia, USSR, Sept. 27, 1951) may be described as follows: muzzle, silvery; face, Caetura (no eye ring); neck, Tilleul Buff; back, Caetura Drab; chest, Caetura; flank stripe, Tilleul Buff; belly, Cartridge Buff; legs, Olive Brown—a strikingly marked animal with extensive shoulder flash. Another bull from Kamchatka (LIZ 24457, Aug. 17, 1911) in earlier pelage may be described as follows: muzzle, white; face, Caetura Black; neck, Tilleul Buff; back, Fuscous Black; flank stripe, Tilleul Buff (restricted); chest, Fuscous Black; belly, Cartridge Buff (restricted); legs, Caetura Drab; tarsal gland, oval, diameter 58, Tilleul Buff; socks and rump patch, restricted.

The females are similarly marked. A female from Karelia was generally browner than a male taken at the same time.

The winter coats of males are much paler. A bull (UHM 637) taken in Karelia, USSR, Jan. 20, 1911, may be described as follows: muzzle, silvery; face, Fuscous Black; cheeks, Snuff Brown; neck, Tilleul Buff; back, Bister; chest, Natal Brown; flank stripe, Tilleul Buff (on shoulder only); belly, Cartridge Buff (restricted); legs, Bister; metatarsal gland, Tilleul Buff, oval, diameter 45; socks, wide, white.

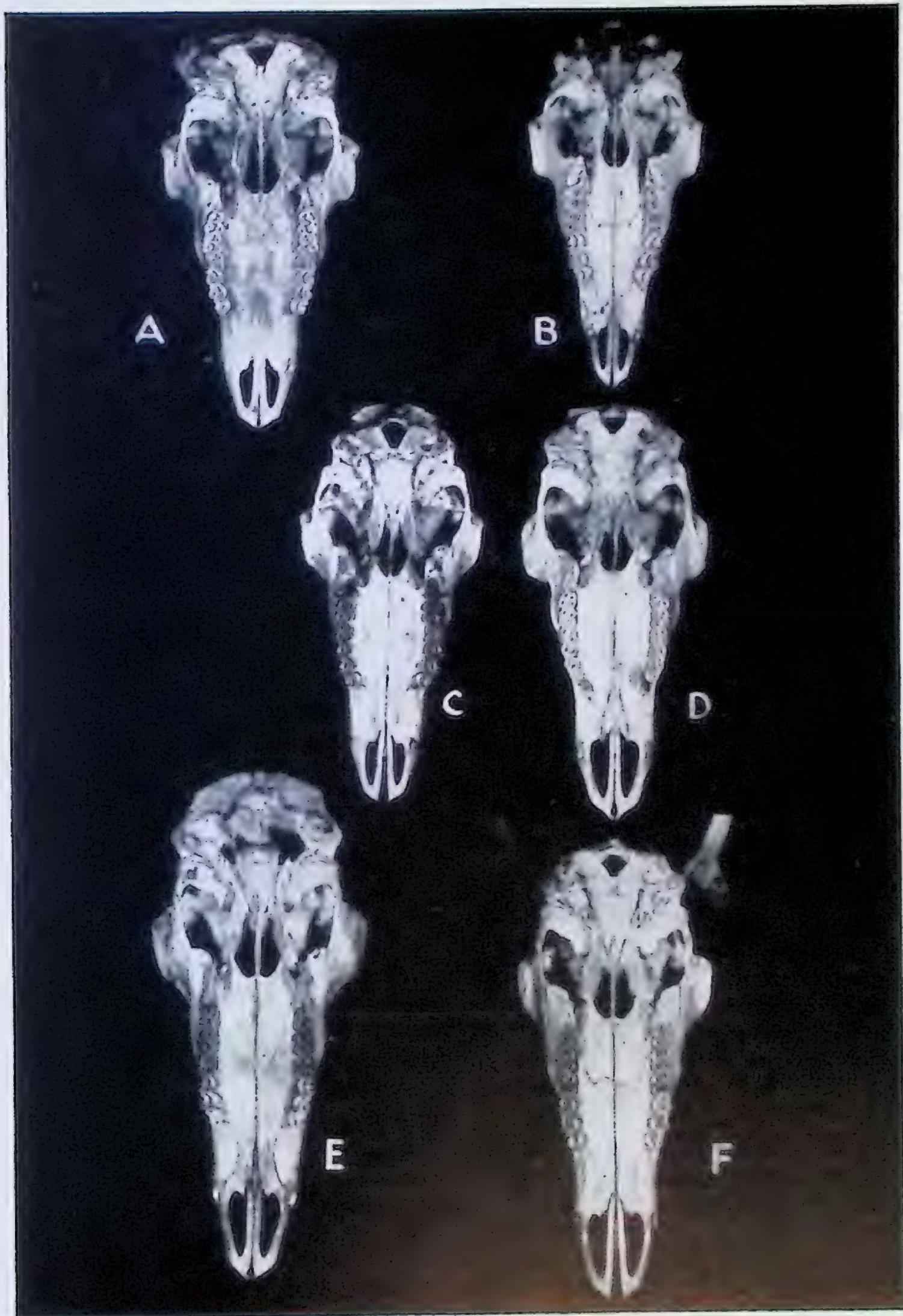
Distribution

The wealth of historical references to reindeer in Europe and Asia, compared to our brief span of knowledge of reindeer in America, makes it difficult to outline contemporaneous distribution. I have chosen to outline the distribution during the latter part of the nineteenth century in the Old World. Although it is slightly earlier than that outlined for the New World, it is approximately comparable as far as pressure of the human population upon the animal life is concerned.

The European distribution was originally outlined by Lonnberg. He quoted Hollsten (1874) as reporting the occurrence of native forest reindeer in northern Sweden around the Gulf of Bothnia. In 1870, Hilden reported wild reindeer in northern Finland from Enontekiö in northwestern Lapland to Inari Lake in the north and east to the Russian boundary. They occupied the forests of Karelia south to the monastery of Valamo in Lake Ladoga. Jacobi (1931) recorded its range as once including the whole of forested Finland.

The following distribution in the Soviet Union has been condensed from Sokolov (1959). The southern boundary led from Lake Ladoga to Lake Ilmen, and Khvoynaya, in Novgorod Province, Vladimir; Makarakskiy, Gorkovskaya Province; latitude 59° north of Kirov, 59° north of Sverdlovsk, also at Krasnoufimsk, west of Sverdlovsk, north of Tyumen and Tobol'sk, near Omsk, Chulyum River (a tributary of the Ob) to Yeniseysk (on the Yenisey), thence to the Angara River and the west shore of Lake Baikal near the headwaters of the Lena River.

Reindeer are also to be found in the Altai-Sayanskiy Mountains from east of Novosibirsk and Semipalatinsk to the southern shore of Lake Baikal. They also occur in extreme northern Outer Mongolia in the Tes River drainage and in the mountains on both sides of Hobsogol Lake. The eastern shore of Lake Baikal is included in the reindeer range as are the highlands



Ventral views of skulls of New World subspecies: (A) *pearyi*, male; (B) *pearyi*, female; (C) *groenlandicus*, male; (D) *groenlandicus*, female; (E) *caribou*, male; (F) *caribou*, female (Scale = $\frac{1}{3}$ ca.).

of Transbaikalia and the upper Vitim River. Reindeer are absent from Chita Province to the south. In Amur Province they occupy the Stanovoy Range, the Burea River valley, and the southern boundary reaches the Okhotsk coast opposite Sakhalin Island at 48° north latitude. The northern limit of forest reindeer would be difficult to define. They occupy the broad taiga belt from the White Sea, Dvina, Mezen, and Pechora river basins, Ob and Yenisey rivers across to the Kolyma River. The distribution includes Sakhalin Island, the Okhotsk coast, and the Kamchatka Peninsula, south of 58° N. latitude.

Status

Exterminated in Sweden about the end of the eighteenth century and in northern Finland about the beginning of the twentieth century (Lonnberg, 1909). Dr. G. Bergman of the Zoological Museum, University of Helsinki, told me that there were still 20 to 40 forest reindeer in Karelia along the Finnish-Soviet border in 1959.

It would be very difficult to arrive at an estimate of the population of this form in the Soviet Union as it is not distinguished from the tundra form in Siberia. According to Sokolov (1959), small herds are still to be found in the taiga of European Russia from Karelia to the Ural Mountains. They are more common in the Siberian taiga between the Yenisey and Kolyma rivers. Shaposhnikov (1955) reported 150 to 200 animals in the Altai Mountains. They are still plentiful in southern Kamchatka where herds up to 1,500 to 2,000 may be observed in the Kronotsky Game Preserve. At the present time, forest reindeer still occupy the northern half of Sakhalin Island from the Shmidt Peninsula to Terpeniya Bay. Herds of up to 50 to 100 animals reach the coast in winter (Sokolov, 1959; after Averin, 1948; and Mishin, 1952).

Taxonomic History

The concept of two kinds of reindeer in the Old World, tundra reindeer and forest reindeer, is very old. Lilljeborg (1874) wrote of Fjellrenen (tundra reindeer) and Skogsrenen (forest reindeer) in Scandinavia. However, it was Lonnberg (1909) who first gave a scientific description of the native forest reindeer of Scandinavia. He carefully distinguished between domestic and native wild reindeer and then identified Linnaeus's *tarandus* as the tundra reindeer of the mountains of western Sweden. That segregated the native lowland forest form of the Gulf of Bothnia for naming. He also concluded that the domestic herds of so-called forest reindeer probably resulted from the introduction of local native forest reindeer breeding stock to the Lapps' domesticated tundra reindeer herds.

Unfortunately, Lonnberg had only two skulls of native wild forest reindeer at his disposal, one from northwestern Finland and one from Karelia in southeastern Finland. His comparative material was also minimal: four *tarandus* skulls from Dalecarlia, Sweden, and one skull from Siberia. However, he recorded most of the skull characteristics which set aside the present subspecies: long, arched, pinched nasals; heavy palmate antlers; long facial portions of skull; large size of animals; and forest habitat. He also mentioned the relatively short tooth row, a not surprising fact because the tooth row is relatively constant for the genus, yet the skull size varies considerably. One of his diagnostic features, the protruding

orbits, has not proved to predominate in the form. His limited sample should be kept in mind in this regard. The present study has disclosed that specimens of *fennicus* from northwest Finland (the site of Lonnberg's type locality) are not typical of forest reindeer populations to the east but rather show certain signs of intergradation (flattened nasals, protruding orbits, and round antler beams) with *tarandus*. It would have been preferable for Lonnberg to have picked the Karelian specimen as typical of Old World forest reindeer. That is why many authors such as Flerov, 1933, and Ellerman and Morrison-Scott (1951) reduced the form to synonymy under *tarandus*. However, from his comparison of *fennicus* with New World woodland caribou it is clear that Lonnberg intended to name the present form in spite of his poor choice of type locality and scanty material.

In 1912, Hollister described the large dark forest reindeer of the Kamchatka Peninsula and Okhotsk coast, based upon a single skull in the United States National Museum.

Millais (1915) named a number of geographical races of Asiatic reindeer without designating types or providing illustrations, thus making it difficult to appraise the status of his names. Three of his names appear to apply to forest reindeer and necessarily come under review in this section. Two of the names were applied to breeds of domestic reindeer and are therefore removed from further consideration.

The trinomial name *chukchensis* was applied to domestic reindeer "from Kolimsk to Bering Strait." The name *yakutskensis* referred to the woodland type domesticated "in the Yakutsk, Amur and Transbaikal" regions. However, Millais applied the name *buskensis* to the native forest reindeer in the Sayanskiy Mountains and the Busk Mountains near Semipalatinsk, Altai region, USSR. He described the skulls as short, massive, resembling *terraenovae*; antlers as short, thick, and much palmated, 35 inches (890) long; length of skull, 12 inches (305), zygomatic breadth, 9 inches (228). It would appear that Flerov (1933 and 1952) was unaware of Millais' names, for he did not compare his *valentinae* from the same region with *buskensis*.

Flerov (1932) described *angustirostris* from the Bargusin Mountains, east of Lake Baikal, as a full species, but reduced it to subspecific rank in 1952. It represented another population of alpine forest caribou of large size and dark pelage. The type specimen has a particularly narrow rostrum with long arched and pinched nasals. The rostrum is so narrow that the ridge of bone surrounding the maxillary tooth row is clearly visible in dorsal aspect. Flerov thought this fact was a diagnostic feature which separated the form from Hollister's *phylarchus*. Unfortunately, Flerov was unable to study the type of *phylarchus*, or he would have found that it, too, had a narrow elongate rostrum with the maxillary tooth row ridge also visible dorsally. Sokolov (1937 and 1959) considered *angustirostris* as a synonym of *phylarchus*, and I concur in his analysis. Flerov (1933) described *setoni*, the native forest reindeer of Sakhalin Island, as a large black-bellied woodland form. However, he later reduced it to synonymy under *phylarchus* (Flerov, 1952), as did Sokolov (1959).

Flerov (1933) described the Siberian forest reindeer as *valentinae* with the type locality in the Altai Mountains east of Semipalatinsk. Unfortunately he chose a yearling male specimen as the type, skin—LIZ 22599, and skull—LIZ 10214, although he reported it as being an adult. That name also



Lateral views of skulls of New World subspecies: (A) *pearyi*, male; (B) *pearyi*, female; (C) *groenlandicus*, male; (D) *groenlandicus*, female; (E) *caribou*, male; (F) *caribou*, female (Scale = $\frac{1}{2}$ ca.).

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For photos of individual skulls -
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represented populations of alpine forest reindeer with long faces and arched nasals. Flerov did not mention antler formation in his diagnosis, since he did not place much faith in that character. Later, this name was applied generally to the forest reindeer of Siberia from the Volga River to the Stanovoy and Jugjur Mountains of Eastern Siberia.

Jacobi (1931) with some hesitancy included forested European Russia as far as the Ural Mountains and the Ob River within the range of *fennicus*. However, Hilzheimer (1936), recognizing Jacobi's hesitancy (op. cit., p. 264, pl. 5) and noting that the figured antlers were decidedly palmate as opposed to specimens from northwest Finland (the type locality of Lonnberg's *fennicus*), described three new races of forest reindeer based on Jacobi's figures. Hilzheimer described *silvicola* from a single antler from Olonetz, Karelskaya, ASSR; *transuralensis*, based on three antlers from the Konda River, Tyumen, USSR; and *dichotomus*, from a single recent antler and a prehistoric one from Orenburg district. Hilzheimer failed to consider variation in antlers or to provide adequate descriptions of his proposed races. His names do not appear to have been considered by Russian authors (Flerov, 1952; Sokolov, 1959), who in general reiterated their earlier classifications.

Remarks

The forest reindeer of Europe and Asia show a similar amount of variation in local populations as found in the woodland caribou of North America. The statistics of various named varieties are compared in Tables 10 and 11. The differences have not proved to be statistically valid according to the methods employed in this study.

Emphasis has been placed upon the forest reindeer of Karelia in this study as typical of Lonnberg's *fennicus*. Similar forest reindeer are to be found eastward to the Ural Mountains. It is a medium-sized dark forest form intergrading with *tarandus* in northwestern Finland and northern Sweden.

The very large dark forest reindeer of Kamchatka, the Okhotsk coast, and Transbaikalia (*phylarchus*), resembles the population of "mountain" caribou in the northern Rocky Mountain region of North America and bears a similar relationship to typical *fennicus*, as *osborni* does to *caribou*. There are indications of intergradation with *tarandus* in the Yakutsk region of northern Siberia.

The forest reindeer of the Altai Mountains, although similar in skull characteristics, are generally paler brown (Shaposhnikoff, 1955). The type of *valentinae* Flerov (LIZ 22599, July 14, 1901) may be described as follows: muzzle, white; face, Buffy Brown; eye ring, Tilleul Buff; neck, Avellaneous; back, Olive Brown; chest, Buffy Brown; flank stripe, Vinaceous Buff; belly, Ivory Yellow; legs, Buffy Brown in front, with posterior stripe Vinaceous Buff; tarsal gland, 63 mm long; length of hooves, 85; width of hooves, 75.

This deme has been placed under *fennicus* with some hesitancy because of the scarcity of specimens. An adequate series of specimens from Tannu Tuva would greatly facilitate the evaluation of this race.

Intergrades Examined

A total of 60 from the following localities: NORWAY: 1 (MCZ). SWEDEN: Pajala, 1 (NRM); Mojärv, 2 (NMR); Swedish Lapland, 2 (NRM), 2 (UCM); Kengis, 5 (NRM). FINLAND: Tornio District, 1 (UHM).

Typical Specimens

FINLAND: Karelia, 2 (UOM). USSR: Karelskaya ASSR, 2 (LIZ); Sortavala, 1 (UHM); Suoyärvi, 2 (UHM); Poroyärvi, 1 (UHM); Reboły, 1 (UHM); Kaitayärvi, 1 (UHM); Olonetz, 1 (UHM); Kazan, 1 (LIZ); Altai, 2 (LIZ); West of Lake Baikal, 1 (LIZ); Transbaikalia, 4 (LIZ); Verkhoyansk, Yana River, 4 (LIZ), 1 (WOM); mouth of Indigirka River, Yakutsk, 5 (LIZ); Sredne Kolymsk, 2 (LIZ); Gizhiga, Okhotsk coast, 2 (AMNH); Kamchatka Peninsula, 8 (LIZ), 1 (USN); Sakhalin Island, 3 (LIZ).

The measurements of a series of five specimens from the Altai region, recorded by Shaposhnikoff (1955), have also been used in the statistical analysis.

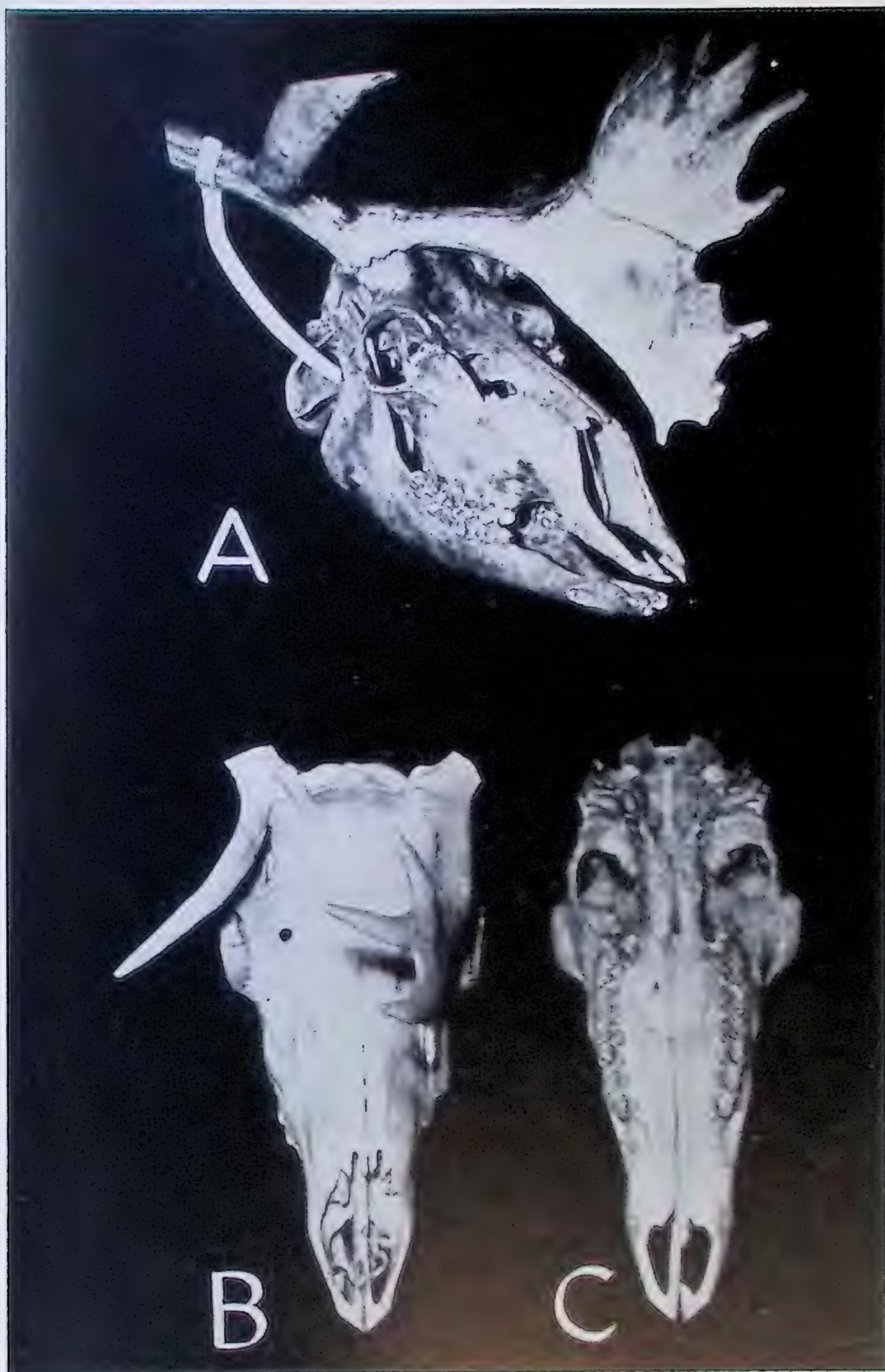
DOMESTIC REINDEER

The domestication of reindeer does not fall within the scope of the present investigation. This section will be limited to a brief review of the recent literature and some comments upon points which have been raised during the present investigation. Readers are referred to Herre (1955) for a recent monograph on the subject.

The history of reindeer husbandry in both the Old and New Worlds has been reviewed by Porsild (1954), who utilized the earlier researches of Laufer (1917) and Mirov (1945). The exact location of the origin of reindeer herding is not known. There are indications that it may have been in southern Siberia east of Lake Baikal. Indeed, there are indications (Maksimov, 1928, and Sokolov, 1937) that reindeer husbandry may have been developed independently by two or more tribes. Nor is the date of its development known. Porsild (op. cit.) reported paintings in the Yakutsk museum, said to have been copied from the walls of caves on the upper Lena River, which depicted human figures, without weapons, walking among reindeer. The original paintings were estimated to be 3,000 years old. Neolithic burials containing reindeer bones and harness accessories are also reported from that area. We do know, from ancient Chinese manuscripts, that reindeer were used as draught animals, beasts of burden, and as a source of milk as early as A.D. 499 in northern Asia.

Reindeer husbandry was brought to northern Europe from Asia by the Lapps some time near the beginning of the Christian Era, for news of domestic reindeer in Scandinavia reached King Alfred's court in England about A.D. 890 through the Viking chieftain Ottar. However, reindeer husbandry was only of secondary importance to hunting, fishing, and trapping in the early years. It was not until after 1600 that the modern Lapp reindeer culture was developed (Vorrin, 1960).

Several basic types of reindeer husbandry are recognized by Mirov (1945), depending upon herding techniques and the various uses made of the animals. Sokolov (1937) distinguished two morphological types of domestic reindeer in the Soviet Union: tundra and forest. The former resembled feral *tarandus* and the latter, *phylarchus*. Domestic tundra reindeer are to be found on the Okhotsk Sea coast and at Kamchatka, and forest reindeer are to be found on parts of the lower Ob and Kasma rivers. Sokolov interpreted those facts as indicating the independent origin of the Chukchi and Koryak cultures and their migrations.



(A) Dorso-lateral view of post-glacial reindeer skull from Villestoft, Denmark (UCM); (B) dorsal view of male skull of *granti*; (C) ventral view of female skull of *granti* (Scale = $\frac{1}{3}$ ca.).

Domestic reindeer were first brought to Alaska in 1891. Porsild states that two separate stocks were imported: a group of larger animals from the Okhotsk coast and smaller animals from the Anadyr region. He picked the larger type for importation to Canada in 1933-35. Their larger size and point of origin may indicate that they possess Asian forest reindeer parentage. This would explain their early rut and calving period. The imported domestic reindeer at the mouth of the Mackenzie River still bear their young as early as April 15, which is about six weeks earlier than the scarce native caribou. This difference in breeding season has been an effective isolating mechanism between the two populations. Hadwen (1932) pointed out that Lapland reindeer bore their young a month before Siberian reindeer.

Reindeer have not been subjected to intensive selective breeding during the period of their domestication. No "breeds" have been developed, such as are found in other species of domestic animals like horses, cattle, sheep, swine, or dogs. Indeed less variation is found in domestic reindeer than in the natural populations of reindeer and caribou. What selection has been practised has been toward larger size and varied colour pattern. White and spotted reindeer are cherished by most herders not only for their colour but as aids in counting their herds.

Up until recently there has been little indication of scientific selective breeding. Indeed, it is a fair generalization to say that the domestic breeds are inferior to the feral populations in size, tooth formation, and general health. Hadwen (1932) came to the same conclusion: "I would unhesitatingly say that under Lapp management the reindeer have degenerated. They do not even compare favourably with the wild species Nevertheless the methods employed have resulted in a smaller animal with less ruggedness than its wild progenitors." During the present investigation domestic reindeer skulls were found to be characterized by small size, light bone structure, and small teeth; whereas field investigations both in northern Canada and in the United Kingdom have indicated a prevalent nutritional deficiency among domestic reindeer herds, which expresses itself in weak bone development.

Domestic reindeer either from Lapland or from eastern Siberian stocks have been transported to many cold regions of the world to start local industries, with mixed results. Some useful references to the various introductions are listed below: Alaska (Leopold and Darling, 1953); Canada (Porsild, 1954); Greenland (Rosing, 1956); Iceland, which had no native reindeer (Laufer, 1917); Orkney Islands (Harper, 1945); Scotland (U. K. Reindeer Council, 1956); and in the Southern Hemisphere, South Georgia (Bonner, 1958) and the Kerguelen Islands.

Specimens Examined

A total of 24 specimens were examined during the current investigation from the following localities: CANADA: Mackenzie River Delta (Siberian stock), 13 (NMC); Labrador (Lapland stock), 11 (NMC).

SUMMARY

This revision will undoubtedly be lightly classified as "lumping" by some readers. Unfortunately, there is still the subjective choice of "lumping" or "splitting" in taxonomic studies. In this case, the decision was initially made to segregate populations which exhibited concordant, statistically valid differences, along with qualitative characters such as antler formation and pelage colour. One could have taken a less exacting point of view and recognized those populations which differed by a single character or showed tendencies toward different antler types or pelage colour. Such populations are treated as demes in this study. As a result of the conservative viewpoint adopted, strong geographical subspecies have been described which may be recognized by other taxonomists with modest series of specimens. In addition, the subspecies will be shown to have evolutionary significance and to permit a certain amount of prediction.

The reindeer and caribou of the world have been shown to belong to a widely distributed, panmictic, plastic superspecies. They share a broadly adaptive genetic pool. The various populations indicate a mosaic pattern of adaptive characters. There are no broad patterns of isophenes typical of centrifugal speciation (Brown, 1957). Indeed, the subspecific pattern appears to fit the conventional concepts of migration and evolution in isolation. However, the species exhibits many of the recently recognized special cases of micro-evolution, such as clines (Huxley, 1940), character displacement (Brown and Wilson, 1956), and evolutionary-senile demes. The relationship between subspecies seems to be that of sharing a common species genetic pool, yet exhibiting an additional group of unique adaptive characters. Such a picture is reminiscent of that outlined by Irwin (1959) for doves of the genus *Streptopelia*.

Reindeer and caribou populations do not readily fit into the classical species and subspecies categories. However, since evolution is a dynamic process, we should not expect to be always able to "freeze" it at the conventional stages. In this case there seem to be several incipient species, two decadent forms and a number of demes below the subspecific level.

Little is known of the earliest remains of *Rangifer* from the earlier glacial periods of western Europe and Alaska. However, in their reappearance during the last Würm-Wisconsin Glaciations, reindeer appeared as a well-adapted dominant indicator of the Arctic fauna, indistinguishable from the existing species. Morphologically, the genus appears to be an early member of the New World Neocervine subfamily. It does not necessarily follow that it originated in North America, but one would look toward the mountainous regions of Alaska or northeastern Asia (Beringia) as the site of origin. As Lindroth (1957) has pointed out, mountains favour speciation because they provide variety of habitats, local zonation, and isolation. The old mountains of northeast Asia are thought to have given rise to a number of hardy boreal species.

Some interesting notes on the rate of subspecific evolution in the genus may be gathered from the geological record. Although there have been no new species evolve in the past 25,000 years or so, there may have been extermination of local races. Compared with existing Alaskan reindeer, the Wisconsin Age reindeer of Alaska, although clearly referable to the tundra reindeer group, show some differences such as tooth row and diastema length.

Specimens from a period about 10,000 to 11,000 years ago indicate an evolution toward present subspecies. Degerbøl and Krog (1959) showed that reindeer from that period in Denmark were similar to the current *tarandus* but had some tendencies toward *fennicus*. In the present study, *constantini* was classified as a forerunner to *fennicus* and *fricki* as an early *caribou* type. Those forms have reached an incipient species level today, and one might predict they would achieve specific status in 25,000 to 10,000 years, if left to their own devices.

Thus, there is some evidence that certain forms have evolved more or less *in situ*. A survey of the present distribution of the subspecies provides some interesting evidence for deducing other points of origin and subsequent migrations. Several levels of differentiation are present in the subspecies, a fact which led to the establishment of the two groups: tundra reindeer (CYLINDRICORNIS) and forest caribou (COMPRESSICORNIS). The first group may be further subdivided into two sub-series: the continental tundra forms and the Arctic island forms, giving three series of approximately the same level of differentiation to consider. Such similar levels of differentiation are thought to indicate similar amounts of isolation.

All the evidence, both historical and taxonomic, points to the conclusion that these three series originated in isolation in separate refugia during the last Würm-Wisconsin glacial phase. Larsen (1958) has listed the many glacial refugia postulated and has divided them into cold tundra and temperate (forest) refugia. It is claimed that the Arctic Island series survived in tundra refugia north of the continental ice-sheets in the Queen Elizabeth Islands, northern Greenland (Peary Land), and possibly on the north coast of Norway (Larsen, 1958, p. 17). There is a confirming Pleistocene record of reindeer for North Greenland. The tundra reindeer are believed to have survived in interglacial and periglacial tundra refugia in Alaska-Yukon (Beringia), western Europe, and possibly northern Siberia (as confirmed by the European and Alaskan specimens). The forest caribou series are thought to have originated in temperate (forest) refugia to the south of the continental ice-sheets (as confirmed by *fricki* and *constantini*). The dominant use of arboreal lichens by woodland caribou (Edwards, Soos, and Ritcey, 1960) is thought to indicate an ecological specialization which might have aided in subspeciation.

Although most of northern North America was covered by ice during the height of the Wisconsin glaciation (Flint, 1957), recent investigations have shown that there were surprisingly large unglaciated regions in the Alaska-Yukon area and Queen Elizabeth Islands of northern Canada. Those regions undoubtedly supported reindeer populations if we can compare the situation to that presently found on the coasts of Greenland.

There are also indications that the Cordilleran and Keewatin glaciers did not reach their maximum extents simultaneously and that an unglaciated

corridor from southern Alberta to the Mackenzie delta was opened at a late period. The present distribution of woodland caribou in the lower Mackenzie Valley is a strong indication that this subspecies occupied the corridor before the tundra reindeer from the Alaskan-Yukon refuge could reach the eastern tundra.

The gradual retreat of the Keewatin Ice-Sheet was followed by an expanding tundra community, which permitted the tundra *groenlandicus* to migrate eastward from a narrow bridgehead in the Mackenzie Delta (perhaps followed by man). The retreat of the ice-sheet from the lower islands of the Canadian Archipelago permitted the Arctic Island basic stock (*pearyi-eogroenlandicus*) to expand its range southward to meet *groenlandicus* on Banks Island, probably while the regions to the eastward were still covered by the glacier. The three main series of reindeer-caribou subspecies in North America therefore re-met in the Mackenzie Delta - Banks Island area at a relatively early date, and since the isolation had not been long enough to permit speciation, they interbred, as presently indicated.

MacNeish's (1955) suggestion of *pearyi* at Great Bear Lake, approximately 5,000 years ago, is open to question. The material is scanty, and A. W. Cameron is now doubtful of the identification.

The eventual melting of the Keewatin Ice-Sheet laid bare the presently occupied realm of *groenlandicus* perhaps within the last 5,000 years. The reindeer were probably quick to take advantage of the new habitat and migrated eastward to claim the continental tundra and eventually island-hop to Baffin Island, Greenland, Southampton, Coats, Mansel Islands, and eventually to reach northwestern Ungava where they met and intergraded with *caribou* again.

It is necessary to consider a final factor that influenced reindeer distribution, i.e., insularity, before we consider the distribution of other races. Certain populations of reindeer and caribou well illustrate the characters, such as dwarfism, shortened legs, rostrums, and antlers (i.e., paedomorphism), which find expression in insular populations of large mammals. If you include Arctic in the definition of the islands and the associated adaptive character, pale coat, you have a fair description of several races of Arctic Island reindeer. Since reindeer are usually gregarious animals, one could normally expect that new islands would be colonized by small herds rather than individuals. Indeed, there are observations of erratic emigrations of herds of reindeer. This greatly increases the chances of the colonization of new range over the chance immigration of single animals. However, even then, the small herd would have a restricted gene pool, and one would expect the rapid evolution of a local deme.

Since Spitsbergen was completely covered by ice during the last glaciation (Lønø, 1959), *platyrhynchus* must be a fairly recent immigrant. There is evidence of current immigration from Novaya Zemlya, and the original immigrants may have come from a northern European tundra refugium, although the distances are great and the ice-bearing currents adverse. It is also possible that the first immigrants reached Spitsbergen from northern Greenland over permanently frozen ice, a distance of about 350 km. Unfortunately, the relationships between the various nearby forms are obscured by the characters associated with insularity, and it is doubtful that a conclusion can be reached on this matter. However, it seems likely

that *platyrhynchus* has fixed its relatively unique characteristics rapidly, because of its small isolated population.

The Queen Charlotte Island caribou *dawsoni* exhibits many of the typical insular characters, but its coat colour and certain skull and antler characteristics proclaim it was woodland caribou isolated on a temperate island.

Both *dawsoni* and *cogroenlandicus* exhibited certain characteristics such as antler abnormalities and smallness of populations which indicate they were evolutionary senile taxa. Those subspecies succumbed during the early part of this century, seemingly without the aid of man.

The relationship between two related forms such as *fennicus* and *caribou*, which have related neighbours to the northward (*tarandus-granti-groenlandicus*), arouses interest. One wonders whether they are patristic (common ancestry) or cladistic (ecologically convergent) groups, as discussed by Cain and Harrison (1960). It was concluded that they were clades, because each seemed to be more closely related to its neighbouring tundra reindeer. Both *tarandus* and *fennicus* appear to share a common gene pool and intergrade locally. The same can be said for *caribou* and *groenlandicus*. The three taxa, *tarandus*, *caribou*, and *fennicus*, are believed to constitute incipient species based upon their history and taxonomic characters. The insular forms *dawsoni* and *platyrhynchus* should be included in the same category because of their degree of differentiation and isolation.

With the above historical background it is intriguing to predict future evolutionary trends, assuming that our own species does not extirpate the various populations. Many of the demes mentioned in the report will reach subspecific rank. The Old World tundra reindeer *tarandus* will have *pearsoni* and possibly *sibiricus* as subspecies. *Platyrhynchus* will be a full species. The forest reindeer *fennicus* will have *buskensis* and *phylarchus* as subspecies. In the New World there may be several new subspecies of tundra reindeer on Baffin and Prince of Wales islands, northern Keewatin District, and northwestern Ungava. The woodland *caribou*, on the other hand, will have *terraenovae*, *caboti*, *sylvestris*, and *stonei* as subspecies.

Р Е З Ю М Е

Данная работа представляет собой таксономический обзор рода северного оленя *Rangifer* во время четвертичного периода, включая как доисторические так и существующие в настоящее время породы. Обзор основан главным образом на размерах черепа. Подвиды различались при наличии совокупности соответствующих характеристик, разнящихся на пятипроцентном уровне значения. Во внимание принимались также неквантитативные характеристики, как цвет шерсти, формирование рогов и биология. Для изучения использован 971 экземпляр, включая около 60 шкур.

Северный олень *Rangifer* принадлежит в *Neocervinae* Crette, которому характерны разделенные внутренние отверстия позвонков и крайние остатки боковых костей плюсны (метаподия). Видимо это был ранний отпрыск типичной группы Нового Мира, которая ведет свое происхождение из северных гор восточной Азии или Аляски. Найдены остатки, принадлежащие к этому роду, относящиеся ко времени второго оледенения в западной Европе (Mindel, т.е. около 440.000 лет тому назад). Он опять появился в начале последнего оледенения (Würm-Wisconsin, приблизительно 120.000 лет тому назад) и явился основным представителем тундровой фауны. Экземпляры северного оленя периода палеолита (25.000 лет) не отличаются от современного вида северного оленя *Rangifer tarandus* (Linnaeus). Классификация доисторического северного оленя принимается следующая:

Rangifer tarandus guettardi Desmarest. Северный олень тундры Европы и Азии.

Rangifer tarandus constantini Flerov. Олень предлесных местностей северной Евразии.

Rangifer tarandus fricki Schultz and Howard. Карибу предлесья северной части Северной Америки.

Rangifer tarandus muscatinensis Leidy. Тундряной олень Северной Америки? (*Incertae sedis*).

Живущие теперь северные олени и карибу составляют пластический панмиктический надвид. Различается девять подвидов, некоторые из них в значительной степени перекрывают друг друга. Подвиды объединяются в две общие группы, которые, вместе с двумя островными формами, считаются достигшими начального уровня выделения видов. Классификация существующих подвидов принимается следующая:

Группа CYLINDRICORNIS Jacobi. А. Тундряной северный олень.

Rangifer tarandus tarandus (Linnaeus). Евразийский тундряной северный олень.

Rangifer tarandus groenlandicus (Linnaeus). Американский тундряной северный олень.

Rangifer tarandus granti Allen. А. Тундряной северный олень Аляски. Б. Северный олень арктических островов.

Rangifer tarandus pearyi Allen. Северный олень Пири.

Rangifer tarandus eogroenlandicus Degerbl. Северный олень северо-восточной Гренландии.

Rangifer tarandus platyrhynchus Vrolik. Северный олень Шпитцбергена.

Группа COMPRESSICORNIS Jacobi. Карибу лесистых местностей.

Rangifer tarandus caribou (Gmelin). Карибу лесистых местностей.

Rangifer tarandus dawsoni Seton. Карибу островов Королевы Шарлотты.

Rangifer tarandus fennicus Lonnberg. Лесной северный олень.

Лесной северный олень и карибу не считаются родственными, а только экологически близкими. Как *dawsoni* так и *platyrhynchus* считаются выделяющимися видами, хотя выделение их могло быть сильно ускорено обитанием на островах. Кроме того, *dawsoni* и *eogroenlandicus* считаются эволюционно устаревшей таксономической группой.

Предполагается, что все три основные группы подвидов получили свое развитие после максимума последнего оледенения, в трех основных неоледеневших районах. Предполагается, что группа, обитающая на арктических островах, формировалась после последнего оледенения в неоледеневшем районе тундры на север от материковых ледовых покровов, на канадских островах Королевы Елизаветы, в северной Гренландии и возможно на северных скандинавских берегах. Предполагается также, что тундряные олени развились в районах неоледеневшей тундры на Аляске—Юконе, западной Европе и возможно в северо-западной Сибири. Предполагается также, что карибу лесных местностей развились в северных неоледеневших районах южнее материковых ледовых покровов в центральной Северной Америке и Азии, а также на островах Королевы Шарлотты. После ухода ледников последовали миграции из этих районов, расселение в новых тундровых местообитаниях, а также переходы на острова через замерзшие проливы. Поскольку изолированные группы оленей не подвергались значительным изменениям, то, при вторичной встрече многих из них, быстро появились смешанные промежуточные породы. В районах совпадающего расселения наблюдается мозаическое разнообразие промежуточных пород и биотипов, а иногда сезонно-географических совпадений и перенос характеристик. Многие местные группы, как названные выше, так и другие, нераспознанные, считаются недостигшими степени подвидов и рассматриваются, как группы таксономически близких особей.

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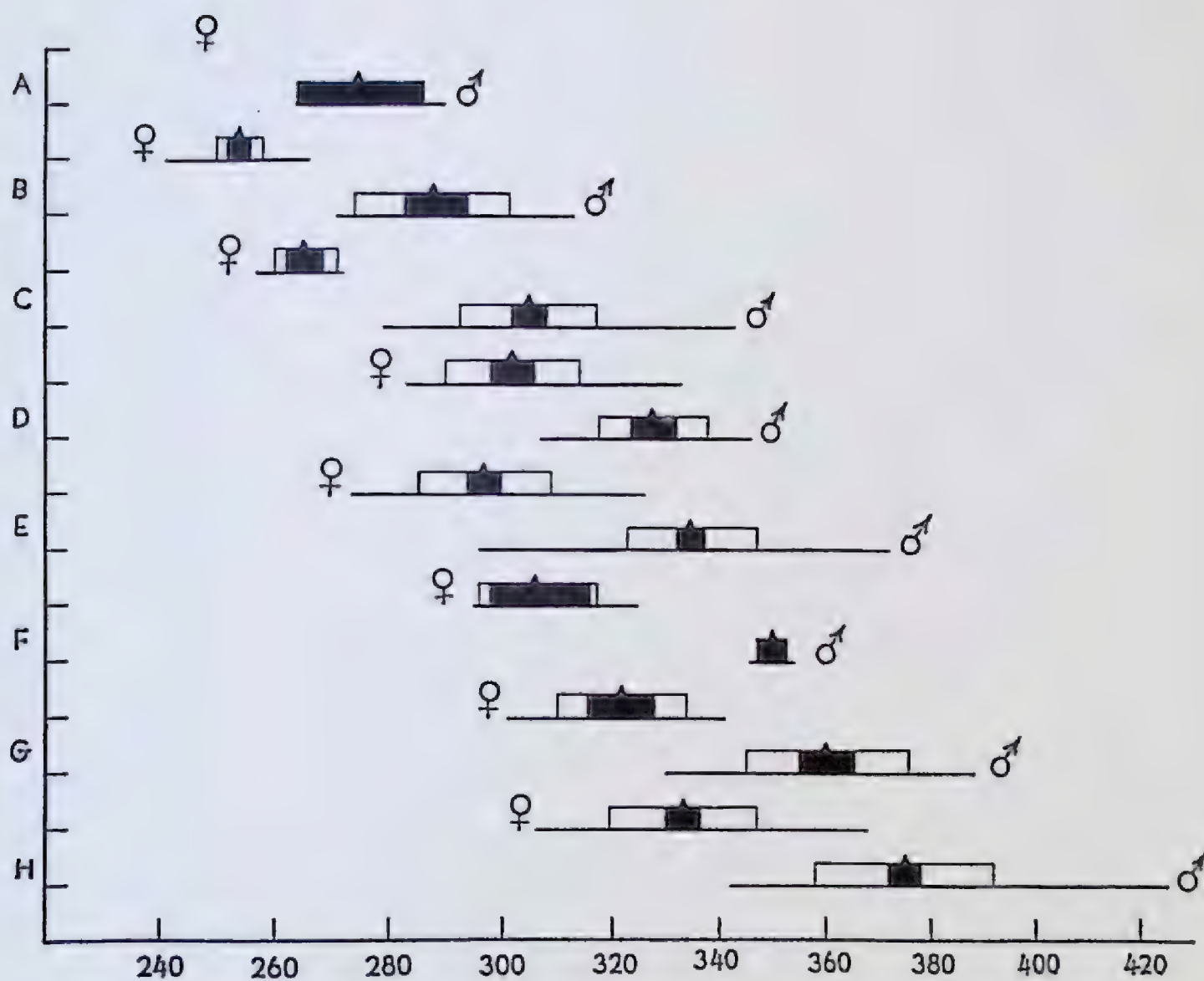


FIGURE 8. Comparison of basal length statistics of the subspecies: A—*cogroenlandicus*, B—*platyrhynchus*, C—*pearyi*, D—*tarandus*, E—*groenlandicus*, F—*granti*, G—*fennicus*, H—*caribou* (No comparable data for *dawsoni*).

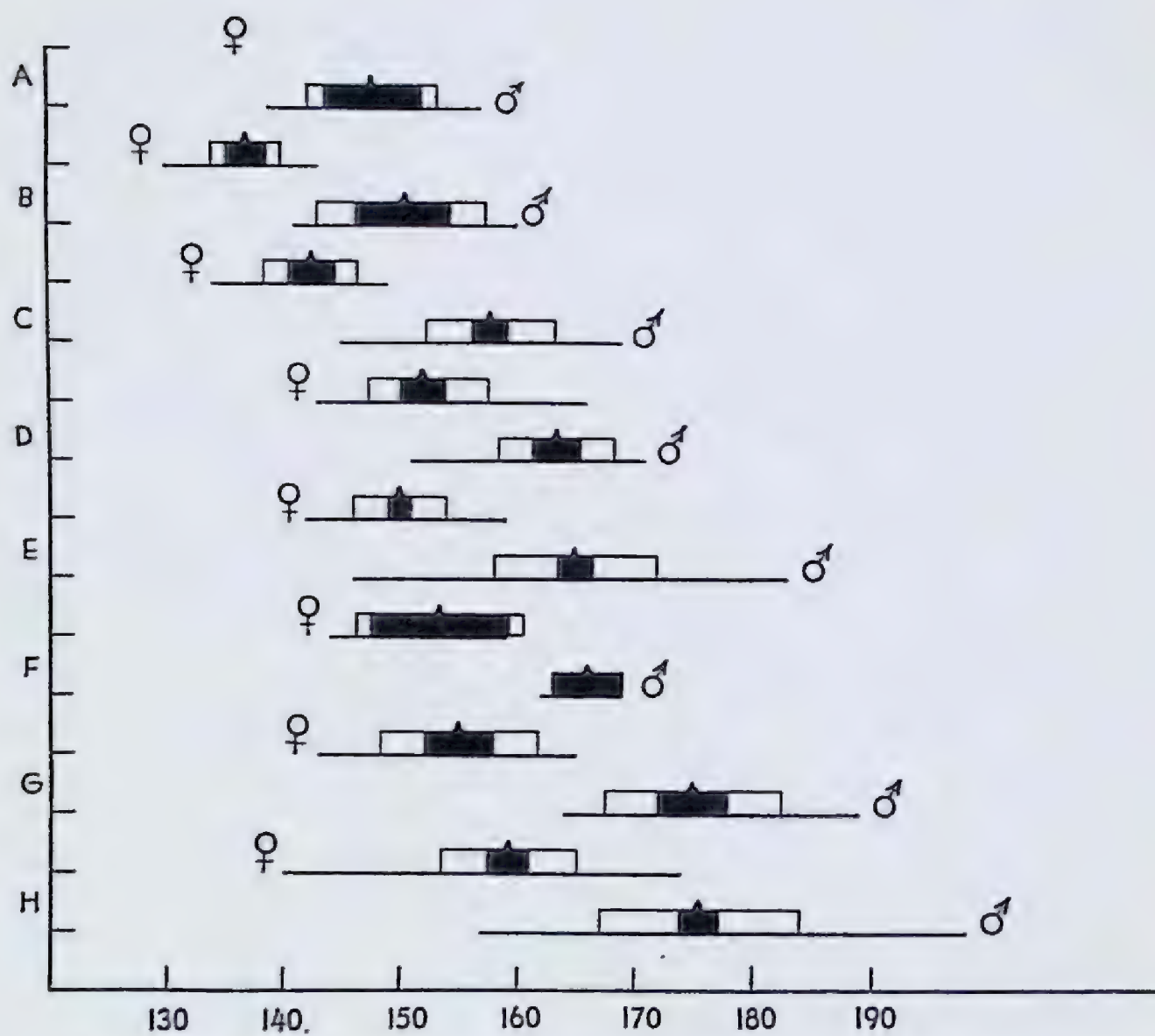


FIGURE 9. Comparison of orbital width statistics of the subspecies. Notation remains the same as in Figure 8.

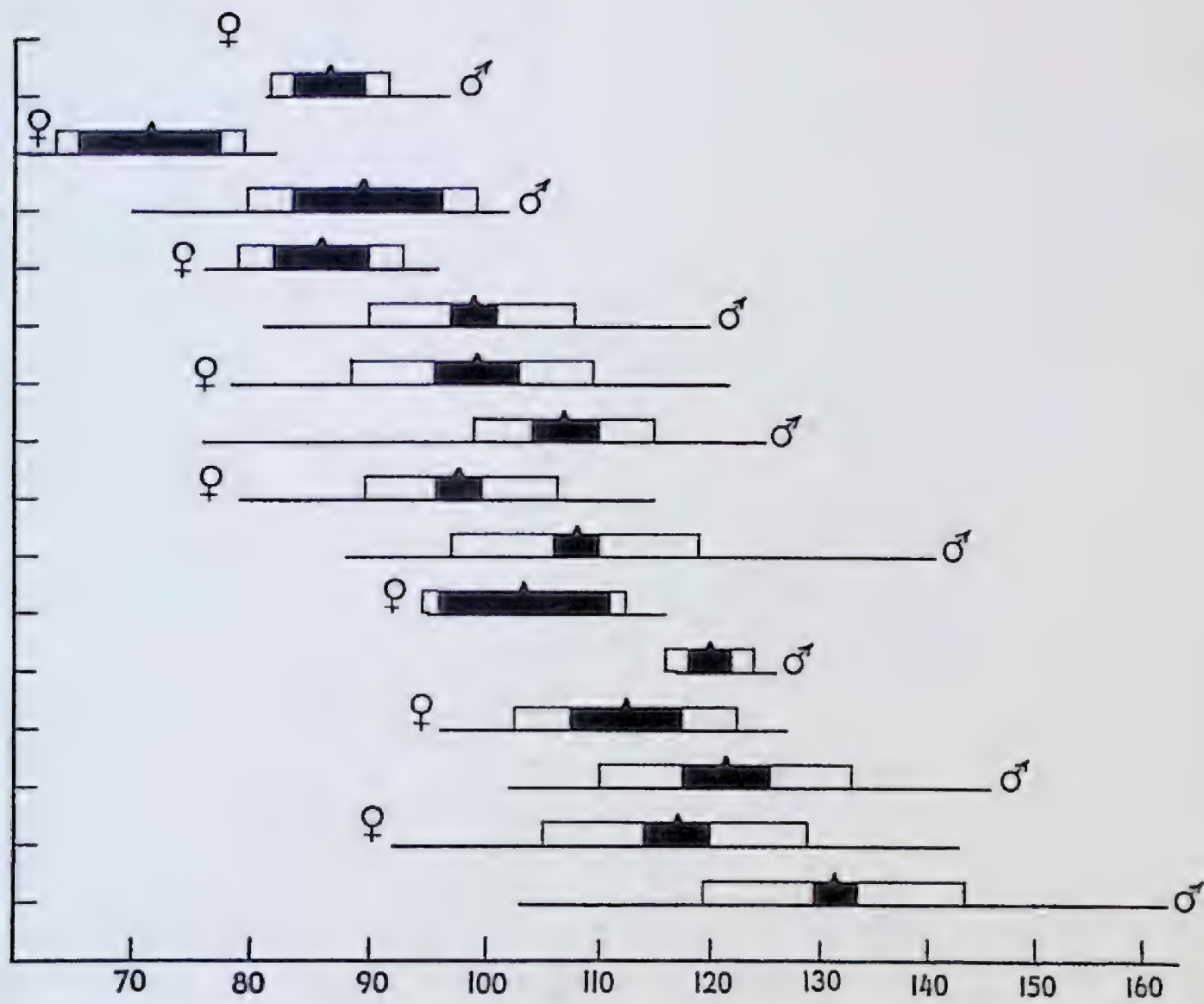


FIGURE 10. Comparison of nasal length statistics of the subspecies. Notation remains the same as in Figure 8.

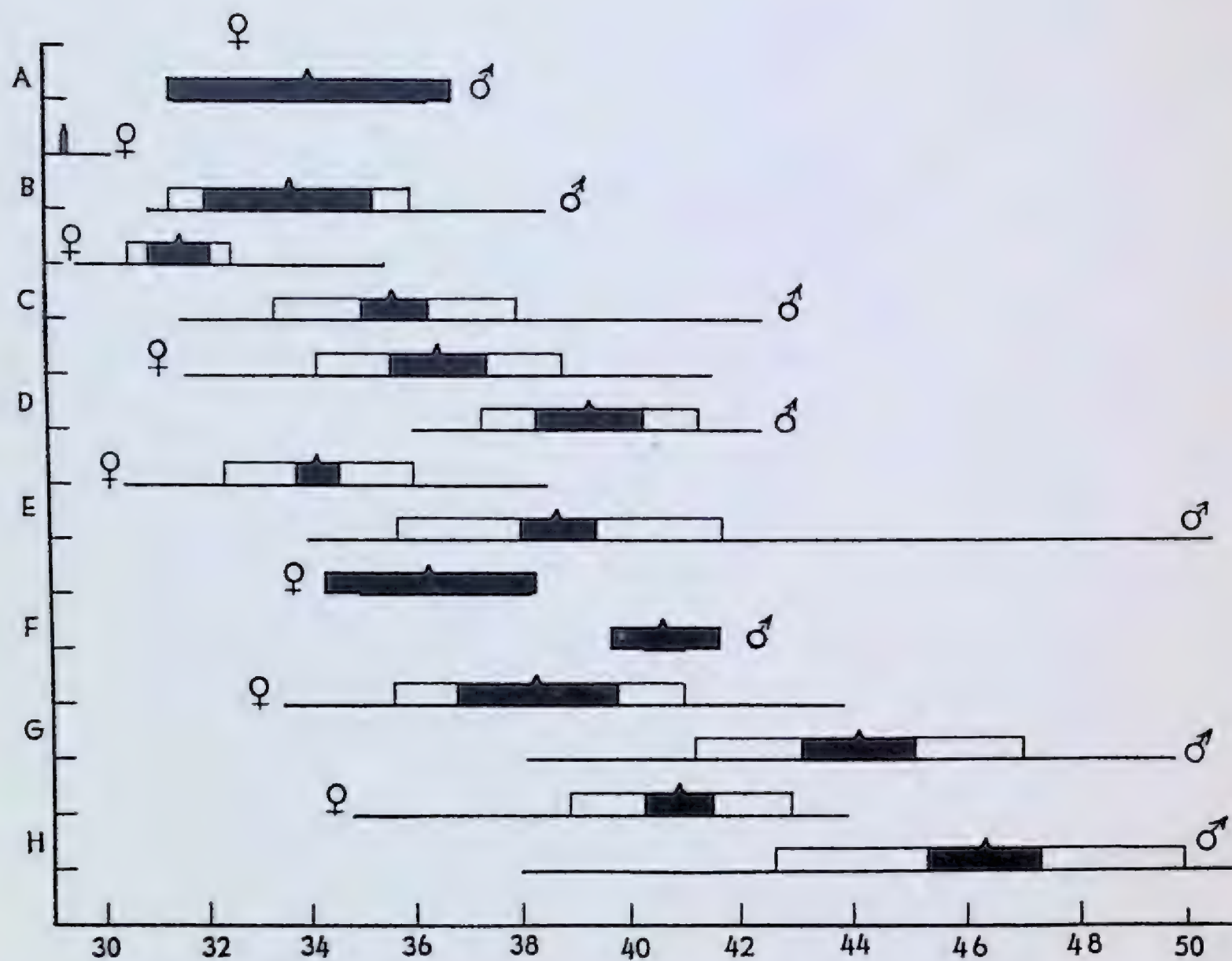


FIGURE 11. Comparison of post nares statistics of the subspecies. Notation remains the same as in Figure 8.

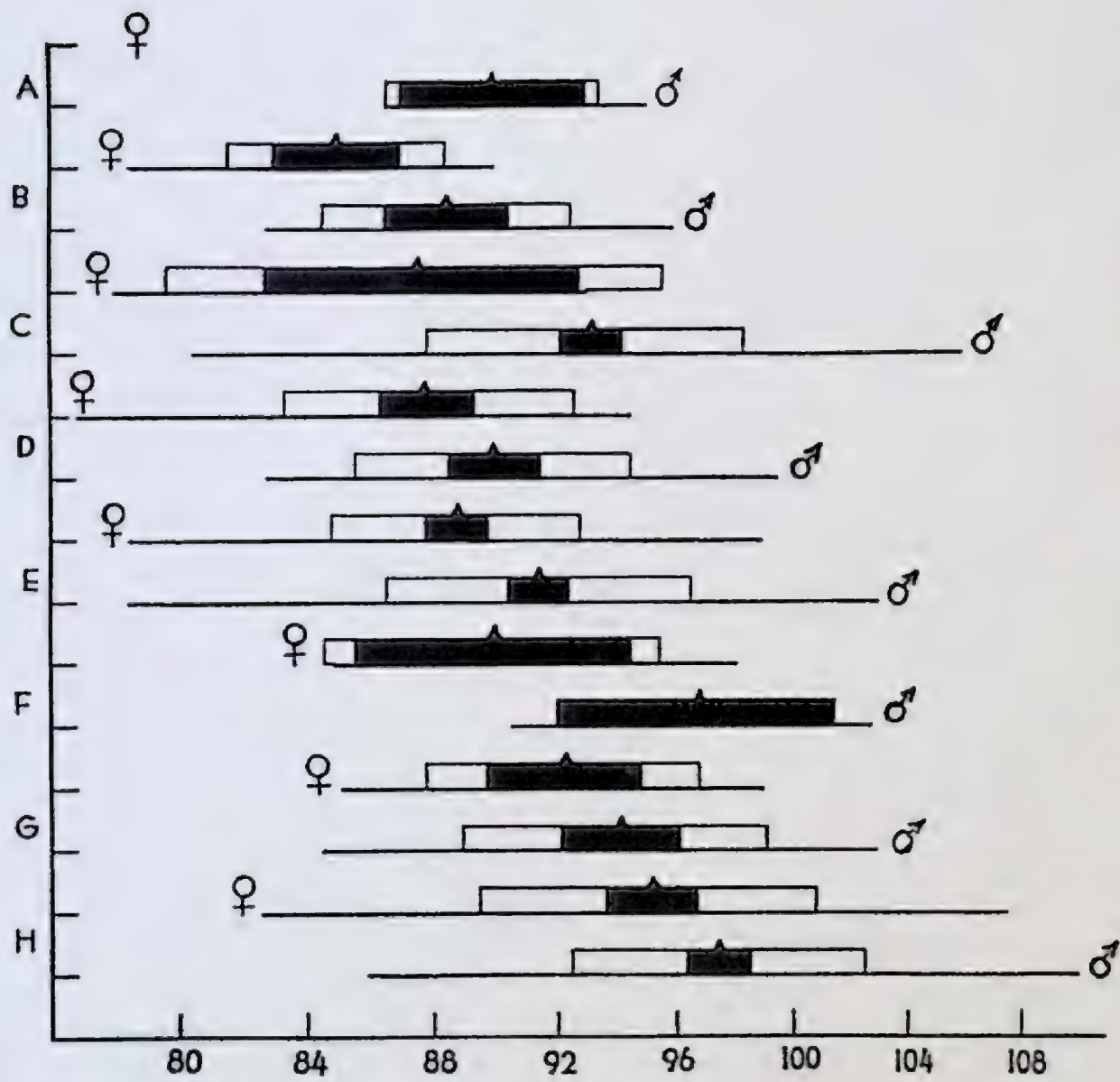


FIGURE 12. Comparison of tooth row statistics of the subspecies. Notation remains the same as in Figure 8.

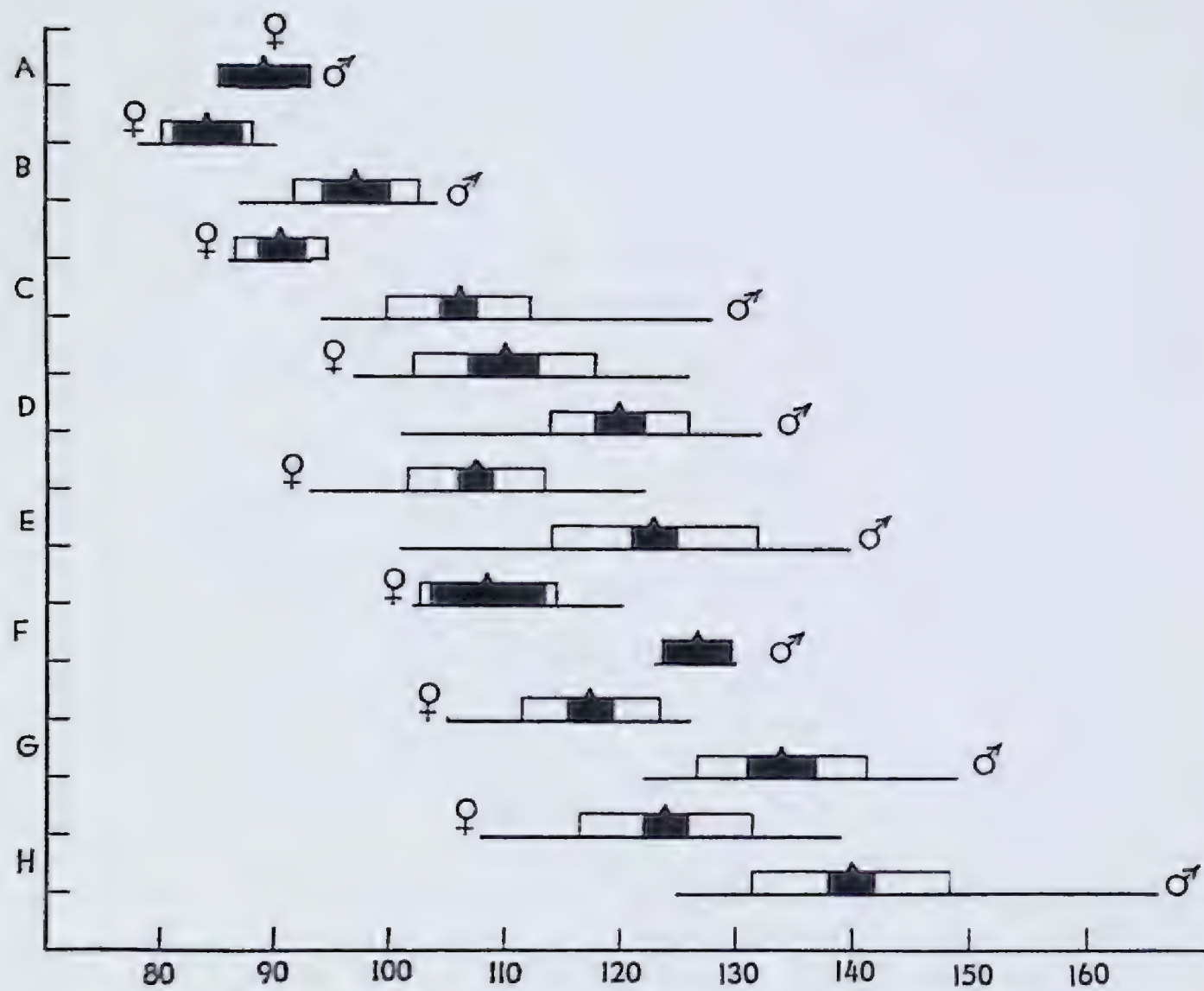


FIGURE 13. Comparison of diastema statistics of the subspecies. Notation remains the same as in Figure 8.

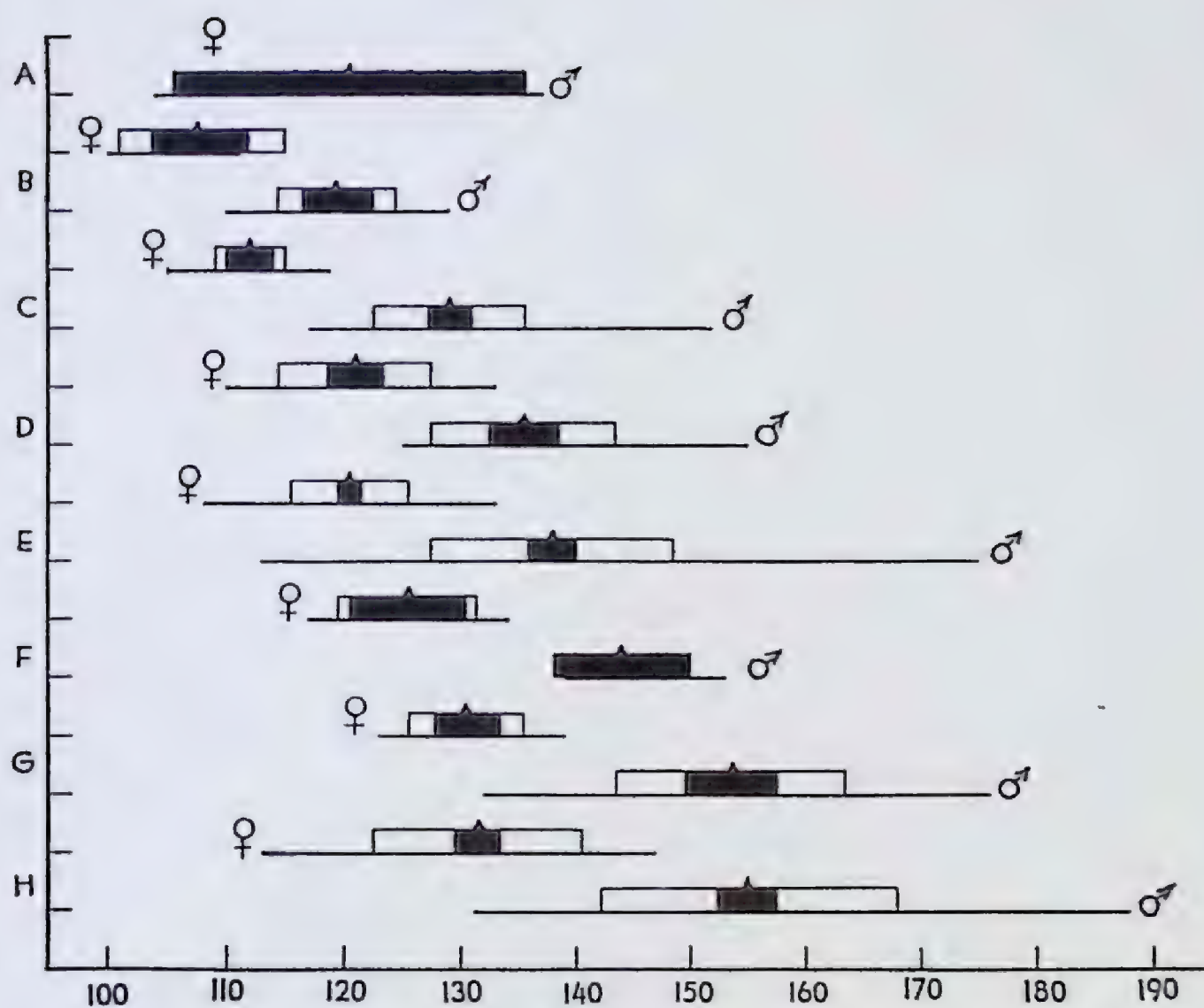


FIGURE 14. Comparison of occipital height statistics of the subspecies. Notation remains the same as in Figure 8.

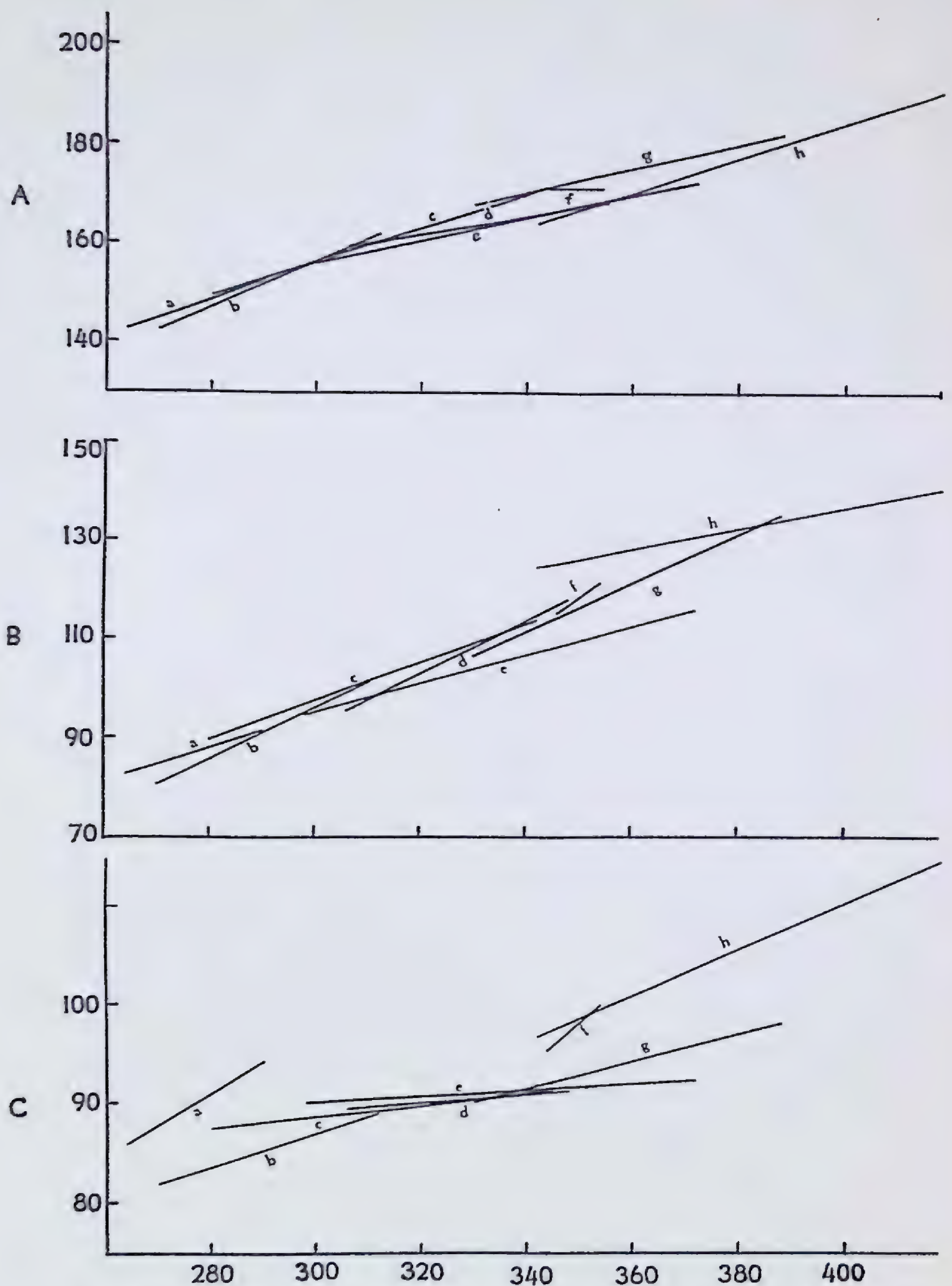


FIGURE 15. Comparison of regression lines for orbital width, nasal length, and tooth row on basal length for males of the subspecies. Notation remains the same as in Figure 8. A, orbital width; B, nasal width; C, tooth row.

APPENDIX I

Table 8. Statistics of Palaearctic Subspecies: Males

Subspecies	n	Range	Mean	S.D.*	S.E.**	C.V.†
BASAL LENGTH						
<i>platyrhynchus</i>	15	271-313	288.1 **	14.48	3.74	5.03
<i>tarandus</i>	29	307-346	327.7 **	10.32	1.91	3.15
<i>fennicus</i>	32	330-388	359.8 **	15.66	2.77	4.35
ORBITAL WIDTH						
<i>platyrhynchus</i>	15	141-160	150.5 **	7.56	1.95	5.02
<i>tarandus</i>	29	151-171	163.4 **	5.18	0.96	3.17
<i>fennicus</i>	32	164-189	175.3 **	7.52	1.33	4.29
NASAL LENGTH						
<i>platyrhynchus</i>	11	70-102	89.6 **	9.69	2.92	10.8
<i>tarandus</i>	29	76-125	107.3 **	8.01	1.49	7.46
<i>fennicus</i>	30	102-146	121.6 **	11.39	2.08	9.33
POST NARES						
<i>platyrhynchus</i>	9	31.0-38.5	33.73**	2.29	0.810	6.79
<i>tarandus</i>	21	36.0-42.5	39.34**	2.05	0.448	5.21
<i>fennicus</i>	26	38.1-49.7	44.08**	2.87	0.563	6.51
TOOTH ROW						
<i>platyrhynchus</i>	15	82.7-95.8	88.56}	3.95	1.02	4.46
<i>tarandus</i>	29	82.7-99.4	90.05}	4.53	0.840	5.03
<i>fennicus</i>	30	84.5-103	94.14**	5.11	0.932	5.42
DIASTEMA						
<i>platyrhynchus</i>	11	87-104	97.1 **	5.68	1.71	5.85
<i>tarandus</i>	27	111-132	120.5 **	6.15	1.18	5.10
<i>fennicus</i>	30	122-149	133.9 **	7.34	1.34	5.47
OCCIPITAL HEIGHT						
<i>platyrhynchus</i>	11	110-129	119.4 **	5.11	1.54	4.29
<i>tarandus</i>	25	125-160	135.4 **	8.13	1.63	6.00
<i>fennicus</i>	30	132-176	153.7 **	9.94	1.81	6.45

* Standard deviation

** Standard error

† Coefficient of variability

Table 9. Statistics of Palaearctic Subspecies: Females

Subspecies	n	Range	Mean	S.D.	S.E.	C.V.
BASAL LENGTH						
<i>platyrhynchus</i>	13	241-266	253.9 **	3.73	1.03	1.47
<i>tarandus</i>	33	283-333	302.2 **	12.36	2.15	4.09
<i>fennicus</i>	16	301-341	321.6 **	12.52	3.13	3.89
ORBITAL WIDTH						
<i>platyrhynchus</i>	13	130-143	137.1 **	3.21	0.889	2.34
<i>tarandus</i>	32	143-166	152.1 *	5.83	1.03	3.83
<i>fennicus</i>	16	143-165	155.1 *	6.85	1.46	4.42
NASAL LENGTH						
<i>platyrhynchus</i>	7	62-82	71.5 **	8.10	3.06	11.3
<i>tarandus</i>	33	78-122	99.3 **	10.51	1.83	10.6
<i>fennicus</i>	14	96-127	112.3 **	9.89	2.64	8.75
POST NARES						
<i>platyrhynchus</i>	5	28.8-30.3	29.40**	0.022	0.001	0.72
<i>tarandus</i>	28	31.7-41.5	36.48*	2.35	0.444	6.44
<i>fennicus</i>	14	33.5-43.8	38.33*	2.67	0.714	6.97
TOOTH ROW						
<i>platyrhynchus</i>	13	78.4-90.0	85.15)	3.37	0.933	3.96
<i>tarandus</i>	33	76.9-94.4	87.89)	4.42	0.770	5.03
<i>fennicus</i>	14	85.2-99.0	92.26*	4.66	1.25	5.05
DIASTEMA						
<i>platyrhynchus</i>	7	78-90	83.6 **	4.00	1.51	4.78
<i>tarandus</i>	32	97-126	110.3 **	7.95	1.41	7.21
<i>fennicus</i>	14	105-126	117.5 **	5.81	0.94	4.52
OCCIPITAL HEIGHT						
<i>platyrhynchus</i>	6	100-111	107.7 **	7.29	1.98	6.75
<i>tarandus</i>	31	110-133	121.2 **	6.60	1.20	5.44
<i>fennicus</i>	14	123-139	130.6 **	4.85	1.30	3.71

Table 10. Statistics of Eurasian Demes: Males

Deme	n	Range	Mean	S.D.	S.E.	C.V.
BASAL LENGTH						
<i>tarandus</i>	12	307-358	326.3	14.9	4.30	4.56
<i>sibiricus</i>	12	322-346	332.9	9.09	2.63	2.73
<i>platyrhynchus</i>	11	272-313	(291.4*)	15.87	4.78	5.45
<i>pearsoni</i>	6	314-337	324.8	9.77	3.99	3.01
<i>fennicus</i>	15	316-379	349.6	21.7	5.60	6.21
<i>valentinae</i>	8	332-363	352.4	10.7	3.78	3.04
<i>angustirostris</i>	3	368-384	378.3	10.2	5.90	2.70
<i>phylarchus</i>	9	333-388	359.9)	19.1	6.37	5.31
ORBITAL WIDTH						
<i>tarandus</i>	12	153-170	163.4	5.90	1.71	3.61
<i>sibiricus</i>	12	151-171	164.6	7.35	2.12	4.47
<i>platyrhynchus</i>	11	142-160	(152.4*)	5.29	1.58	3.34
<i>pearsoni</i>	6	157-164	161.3	4.34	1.77	2.70
<i>fennicus</i>	15	154-188	174.4)	9.39	2.43	5.40
<i>valentinae</i>	8	168-187	173.1	8.17	2.89	4.72
<i>angustirostris</i>	3	174-189	180.3	8.86	5.12	4.91
<i>phylarchus</i>	9	165-184	173.0)	6.96	2.32	4.02

Table 10. Statistics of Eurasian Demes: Males (Cont'd)

Deme	n	Range	Mean	S.D.	S.E.	C.V.
NASAL LENGTH						
<i>tarandus</i>	12	95.3-120	108.0	7.12	2.06	6.59
<i>sibiricus</i>	12	104-125	111.9	7.50	2.17	6.70
<i>platyrhynchus</i>	11	70-102	89.6	9.69	2.92	10.8
<i>pearsoni</i>	6	76.4-112	96.0	19.95	8.14	20.78
<i>fennicus</i>	15	100-146	120.0	14.45	3.73	12.0
<i>valentinae</i>	6	110-123	114.8	5.00	2.04	4.39
<i>angustirostris</i>	3	117-134	123.7	8.60	4.97	6.93
<i>phylarchus</i>	9	102-138	121.6	13.5	4.50	11.08
POST NARES						
<i>tarandus</i>	7	37.2-41.9	40.20	2.00	0.754	4.97
<i>sibiricus</i>	8	36.0-42.5	39.24	2.42	0.855	6.17
<i>platyrhynchus</i>	9	31.0-38.5	(33.73*)	2.29	0.810	6.79
<i>pearsoni</i>	6	36.4-40.5	38.47	1.18	0.481	3.06
<i>fennicus</i>	13	39.3-49.7	44.02	3.17	0.878	7.20
<i>valentinae</i>	6	39.5-47.2	43.72	2.79	1.14	6.38
<i>angustirostris</i>	3	43.3-47.0	44.57	3.00	1.73	6.72
<i>phylarchus</i>	7	38.1-47.0	42.87	3.27	1.23	7.62
MAXILLARY TOOTH ROW						
<i>tarandus</i>	12	83.5-99.4	89.58	5.20	1.50	5.80
<i>sibiricus</i>	12	82.7-95.5	89.84	4.32	1.25	4.81
<i>platyrhynchus</i>	11	82.7-95.8	88.67	4.37	1.32	4.93
<i>pearsoni</i>	6	84.0-94.5	91.28	4.07	1.66	4.46
<i>fennicus</i>	15	84.5-98.9	91.65	4.15	1.07	4.53
<i>valentinae</i>	6	90.5-101	95.38	4.40	1.80	4.61
<i>angustirostris</i>	3	96.9-101	99.30	2.28	1.33	2.30
<i>phylarchus</i>	9	86.1-103	94.21	6.15	2.05	6.53
INCISIVE FORAMEN						
<i>tarandus</i>	10	44.3-54.2	48.57	3.65	1.15	7.51
<i>sibiricus</i>	10	45.0-55.2	50.72	1.31	0.415	2.58
<i>platyrhynchus</i>	10	40.5-52.3	44.00	3.48	1.10	7.91
<i>pearsoni</i>	6	45.8-50.5	48.05	1.61	0.657	3.35
<i>fennicus</i>	15	39.0-62.0	52.06	5.81	1.50	11.16
<i>valentinae</i>	6	50.5-59.0	55.43	3.58	1.46	6.46
<i>angustirostris</i>	3	55.3-57.7	58.90	2.00	1.16	3.40
<i>phylarchus</i>	9	50.2-63.5	55.06	4.29	1.43	7.78
DIAPYSTEMA LENGTH						
<i>tarandus</i>	10	111-135	117.3	7.08	2.24	6.04
<i>sibiricus</i>	12	118-132	124.9	5.39	1.56	4.31
<i>platyrhynchus</i>	11	873-104	(97.09*)	5.68	1.71	5.85
<i>pearsoni</i>	6	112-126	119.5	5.39	2.20	4.51
<i>fennicus</i>	15	114-149	130.4	11.03	2.85	8.46
<i>valentinae</i>	6	125-139	131.3	5.59	2.28	4.26
<i>angustirostris</i>	3	126-143	135.0	8.54	4.94	6.33
<i>phylarchus</i>	9	122-149	133.2	9.27	3.09	6.96
OCCIPITAL HEIGHT						
<i>tarandus</i>	8	125-157	138.6	10.58	3.74	7.63
<i>sibiricus</i>	12	127-160	136.6	10.75	3.11	7.87
<i>platyrhynchus</i>	11	110-129	(119.4*)	5.11	1.54	4.29
<i>pearsoni</i>	6	129-141	132.3	5.65	2.31	4.28
<i>fennicus</i>	15	133-168	150.3	11.40	2.95	7.58
<i>valentinae</i>	6	143-159	149.8	7.25	2.96	4.83
<i>angustirostris</i>	3	144-157	152.3	8.25	4.77	5.42
<i>phylarchus</i>	9	132-176	154.3	15.78	5.26	10.23

Table 11. Statistics of Eurasian Demes: Females

Deme	n	Range	Mean	S.D.	S.E.	C.V.
BASAL LENGTH						
<i>tarandus</i>	10	284-322	300.8	11.6 12.75 8.62 7.96 20.7 9.64 17.7 12.7	3.67	3.86
<i>sibiricus</i>	17	283-333	305.9		3.09	4.17
<i>platyrhynchus</i>	7	241-266	(252.0*)		3.25	3.42
<i>pearsoni</i>	6	290-301	293.8		3.25	2.71
<i>fennicus</i>	5	275-329	302.0		9.24	6.85
<i>valentinae</i>	4	315-337	324.2		4.82	2.98
<i>angustirostris</i>	2	308-333	320.5		12.6	5.52
<i>phylarchus</i>	5	308-341	326.8		5.67	3.89
ORBITAL WIDTH						
<i>tarandus</i>	10	148-158	151.8	8.54 6.47 1.63 2.29 5.89 3.96 8.49 6.56	2.70	5.63
<i>sibiricus</i>	17	143-166	152.8		1.57	4.23
<i>platyrhynchus</i>	7	130-143	(135.9*)		0.615	1.20
<i>pearsoni</i>	5	148-154	150.2		1.02	1.52
<i>fennicus</i>	5	145-159	150.8		2.63	3.93
<i>valentinae</i>	4	154-163	158.7		1.98	2.49
<i>angustirostris</i>	2	153-165	159.0		6.02	5.33
<i>phylarchus</i>	5	150-165	157.4		2.93	4.17
NASAL LENGTH						
<i>tarandus</i>	10	94-114	102.9	5.49 12.32 8.10 5.92 6.52 8.09 17.7 9.75	1.74	5.34
<i>sibiricus</i>	17	78-112	100.3		2.99	12.3.
<i>platyrhynchus</i>	7	62-82	(71.5*)		3.06	11.3
<i>pearsoni</i>	6	80-95	90.33		2.42	6.55
<i>fennicus</i>	5	95-110	101.2		2.91	6.44
<i>valentinae</i>	3	108-122	116.3		4.68	6.97
<i>angustirostris</i>	2	103-128	115.5		12.6	15.32
<i>phylarchus</i>	5	105-129	115.4		4.35	8.45
POST NARES						
<i>tarandus</i>	8	34.2-39.8	37.34	2.00 2.94 0.224 0 1.41 3.67 3.16 2.89	0.707	5.36
<i>sibiricus</i>	15	31.7-41.5	36.35		0.760	8.09
<i>platyrhynchus</i>	5	28.8-30.3	(29.4*)		0.001	0.72
<i>pearsoni</i>	5	35.0-36.4	35.48		0	0
<i>fennicus</i>	5	35.7-39.2	37.62		0.629	3.75
<i>valentinae</i>	3	37.1-43.8	39.53		2.12	9.29
<i>angustirostris</i>	2	33.5-38.1	35.80		2.24	8.83
<i>phylarchus</i>	4	36.5-43.3	39.57		1.445	7.30
MAXILLARY TOOTH ROW						
<i>tarandus</i>	10	84.5-91.2	87.33	3.70 4.95 3.24 3.92 4.09 7.94 1.00 1.12	1.17	4.24
<i>sibiricus</i>	17	76.9-93.5	87.17		1.20	5.68
<i>platyrhynchus</i>	7	78.4-88.0	83.86		1.22	3.86
<i>pearsoni</i>	6	83.6-94.4	90.88		1.60	4.31
<i>fennicus</i>	5	79.5-90.5	85.34		1.83	4.79
<i>valentinae</i>	3	83.2-99.0	91.13		4.59	8.71
<i>angustirostris</i>	2	92.7-94.2	93.45		0.709	1.07
<i>phylarchus</i>	5	92.1-95.1	93.84		0.500	1.19
INCISIVE FORAMEN						
<i>tarandus</i>	9	38.7-50.2	45.59	3.97 4.09 2.31 5.22 5.85 4.58 0 2.60	1.32	8.71
<i>sibiricus</i>	17	40.0-56.3	47.33		0.993	8.64
<i>platyrhynchus</i>	7	34.7-40.8	(37.23*)		0.872	6.20
<i>pearsoni</i>	6	40.8-54.8	45.12		2.13	11.57
<i>fennicus</i>	5	36.0-51.0	42.96		2.61	13.60
<i>valentinae</i>	3	45.8-54.5	49.50		2.65	9.20
<i>angustirostris</i>	2	47.3-47.8	47.55		0	0
<i>phylarchus</i>	5	44.6-51.3	47.80		1.16	5.44

Table 11. Statistics of Eurasian Demes: Females (Cont'd)

Deme	n	Range	Mean	S.D.	S.E.	C.V.
DIASTEMA LENGTH						
<i>tarandus</i>	9	97-117	107.6	5.40	1.80	5.02
<i>sibiricus</i>	17	98-126	114.2	7.38	1.79	6.47
<i>platyrhynchus</i>	7	78-90	(83.6*)	4.00	1.51	4.78
<i>pearsoni</i>	6	98-107	103.5	3.20	1.31	3.09
<i>fennicus</i>	5	98-120	108.0	10.42	4.65	9.65
<i>valentinae</i>	3	116-125	120.0	4.58	2.65	3.82
<i>angustirostris</i>	2	111-122	116.5	7.81	5.54	6.70
<i>phylarchus</i>	5	109-126	118.4	6.06	2.71	5.12
OCCIPITAL HEIGHT						
<i>tarandus</i>	8	113-138	122.1	7.85	2.77	6.43
<i>sibiricus</i>	17	110-133	122.7	6.72	1.63	5.48
<i>platyrhynchus</i>	6	100-111	107.7	7.29	1.98	6.75
<i>pearsoni</i>	6	112-120	115.8	4.45	1.82	3.84
<i>fennicus</i>	5	115-134	128.2	7.68	3.43	6.00
<i>valentinae</i>	3	130-141	134.0	6.08	2.62	4.54
<i>angustirostris</i>	2	123-132	127.5	6.40	4.54	5.02
<i>phylarchus</i>	5	125-139	130.2	5.41	2.42	4.16

Table 12. Statistics of Nearctic Subspecies: Males

Subspecies	n	Range	Mean	S.D.	S.E.	C.V.
BASAL LENGTH						
<i>cogroenlandicus</i>	4	264-290	275.0 **	10.98	5.49	3.99
<i>pearyi</i>	64	279-343	304.6 **	12.53	1.57	4.11
<i>groenlandicus</i>	108	296-372	334.1 *	15.63	1.50	4.68
<i>granti</i>	4	346-354	349.7 *	3.32	1.66	0.95
<i>caribou</i>	112	342-427	374.3 **	16.96	1.60	4.53
ORBITAL WIDTH						
<i>cogroenlandicus</i>	8	139-157	147.7 **	5.42	1.92	3.67
<i>pearyi</i>	65	145-169	157.7 *	5.63	0.665	3.40
<i>groenlandicus</i>	105	146-183	164.8)	7.21	0.703	4.37
<i>granti</i>	4	162-169	166.2)	3.11	1.55	1.87
<i>caribou</i>	114	157-198	175.5 **	8.66	0.811	4.94
NASAL LENGTH						
<i>cogroenlandicus</i>	8	81-97	86.7 **	4.88	1.72	5.63
<i>pearyi</i>	65	81-120	99.1 *	9.01	1.13	9.09
<i>groenlandicus</i>	108	88-141	108.2 *	10.84	1.04	10.02
<i>granti</i>	4	117-126	120.2 *	4.04	2.02	3.37
<i>caribou</i>	116	103-163	131.4 *	12.26	1.14	9.33
POST NARES						
<i>cogroenlandicus</i>	3	31.5-36.3	34.07)	2.34	1.35	6.86
<i>pearyi</i>	61	31.6-42.4	35.65)	2.28	0.294	6.40
<i>groenlandicus</i>	72	34.0-51.5	38.74)	3.06	0.360	7.90
<i>granti</i>	2	40.3-41.0	40.65)	1.00	0.500	2.46
<i>caribou</i>	55	38.0-56.2	46.27 **	3.70	0.499	8.00
TOOTH ROW						
<i>cogroenlandicus</i>	4	86.5-95.0	89.92)	3.56	1.78	3.96
<i>pearyi</i>	61	80.3-106	93.13)	5.30	0.684	5.69
<i>groenlandicus</i>	92	78.2-103	91.44)	4.99	0.520	5.46
<i>granti</i>	4	90.5-103	96.85)	5.10	2.55	5.26
<i>caribou</i>	111	85.7-110	97.40)	5.03	0.478	5.16
DIASTEMA						
<i>cogroenlandicus</i>	2	87-91	89.0 **	2.83	2.01	3.18
<i>pearyi</i>	62	94-128	106.1 **	6.33	0.804	5.97
<i>groenlandicus</i>	85	101-140	122.9)	8.79	0.953	7.15
<i>granti</i>	4	123-130	126.7)	3.21	1.60	2.35
<i>caribou</i>	112	125-166	140.0 **	8.64	0.817	6.17
OCCIPITAL HEIGHT						
<i>cogroenlandicus</i>	4	104-137	120.5)	15.15	7.57	12.57
<i>pearyi</i>	63	117-152	129.1)	6.66	0.839	5.16
<i>groenlandicus</i>	85	113-175	137.7)	10.61	1.15	7.70
<i>granti</i>	4	139-153	144.2)	6.08	3.04	4.22
<i>caribou</i>	99	131-188	155.2 *	12.78	1.28	8.23

Table 13. Statistics of Nearctic Subspecies: Females

Subspecies	n	Range	Mean	S.D.	S.E.	C.V.
BASAL LENGTH						
<i>cogroenlandicus</i>	1		253			
<i>pearyi</i>	14	257-272	265.4**	5.48	1.47	2.06
<i>groenlandicus</i>	82	273-326	296.9**	12.12	1.34	4.08
<i>granti</i>	6	295-325	306.2**	9.91	4.04	3.24
<i>caribou</i>	65	306-368	333.4**	13.77	1.71	4.13
ORBITAL WIDTH						
<i>cogroenlandicus</i>	1		138			
<i>pearyi</i>	14	134-149	142.4**	4.09	1.09	2.87
<i>groenlandicus</i>	82	142-159	149.9)	3.99	0.44	2.66
<i>granti</i>	6	144-159	153.3)	7.16	2.92	4.67
<i>caribou</i>	65	140-174	159.3**	5.81	0.72	3.64
NASAL LENGTH						
<i>cogroenlandicus</i>	1		80			
<i>pearyi</i>	14	76-96	86.1**	7.01	1.87	8.14
<i>groenlandicus</i>	80	79-115	97.7)	8.33	0.93	8.53
<i>granti</i>	6	95-116	103.3)	8.67	3.54	8.39
<i>caribou</i>	65	92-143	116.9**	11.68	1.45	9.99
POST NARES						
<i>cogroenlandicus</i>	1		33.2			
<i>pearyi</i>	12	29.6-35.5	31.58**	1.00	0.289	3.16
<i>groenlandicus</i>	73	30.5-38.5	34.22*	1.78	0.208	5.20
<i>granti</i>	3	35.0-38.2	36.30**	2.00	1.16	5.51
<i>caribou</i>	38	34.8-43.9	40.88**	1.98	0.321	4.84
TOOTH ROW						
<i>cogroenlandicus</i>	1		79.5			
<i>pearyi</i>	12	78.0- 93.0	87.69)	8.20	2.37	9.35
<i>groenlandicus</i>	80	78.3- 99.0	88.78)	3.97	0.443	4.47
<i>granti</i>	6	84.9- 98.1	90.00)	5.60	2.29	6.22
<i>caribou</i>	63	82.5-107	95.24**	5.65	0.712	5.93
DIASTEMA						
<i>cogroenlandicus</i>	1		92			
<i>pearyi</i>	12	86-93	90.5**	3.91	1.13	4.33
<i>groenlandicus</i>	76	93-122	107.6)	5.84	.67	5.43
<i>granti</i>	6	102-120	108.7)	6.03	2.46	5.35
<i>caribou</i>	57	108-139	124.2 **	7.47	0.989	6.01
OCCIPITAL HEIGHT						
<i>cogroenlandicus</i>	1		111			
<i>pearyi</i>	12	105-119	111.9 **	3.33	0.962	2.98
<i>groenlandicus</i>	76	108-133	120.6 *	5.28	0.606	4.38
<i>granti</i>	6	117-134	125.7 *	6.07	2.48	4.82
<i>caribou</i>	60	113-147	131.6 *	8.83	1.14	6.71

Table 14. Statistics of *Rangifer t. groenlandicus* Male Demes

Deme	n	Range	Mean	S.D.	S.E.	C.V.
BASAL LENGTH						
<i>groenlandicus</i>	33	298-372	338.5)	17.35	3.02	5.13
<i>keewatinensis</i>	21	321-372	343.2)	14.14	3.09	4.12
<i>arcticus</i>	54	293-353	328.9)	13.31	1.78	4.02
ORBITAL WIDTH						
<i>groenlandicus</i>	33	150-175	166.2)	6.12	1.07	3.69
<i>keewatinensis</i>	21	156-183	168.2)	7.28	1.58	4.32
<i>arcticus</i>	51	146-175	162.5)	6.81	0.954	4.19
NASAL LENGTH						
<i>groenlandicus</i>	16	88-119	103.0	9.42	1.65	9.15
<i>arcticus</i>	75	96-141	110.5	10.70	1.24	9.68
POST NARES						
<i>groenlandicus</i>	11	35.0-51.5	40.62)	5.12	1.54	12.6
<i>arcticus</i>	61	34.0-43.6	38.40)	2.46	0.315	6.41
TOOTH ROW						
<i>groenlandicus</i>	15	78.2-101.2	91.12)	6.30	1.52	6.91
<i>arcticus</i>	75	79.0-100.0	91.51)	4.72	0.545	5.16
DIASTEMA						
<i>groenlandicus</i>	16	104-140	121.6)	10.50	2.62	8.63
<i>arcticus</i>	69	101-138	123.2)	8.41	1.01	6.82
OCCIPITAL HEIGHT						
<i>groenlandicus</i>	15	113-175	144.9)	15.5	4.01	10.70
<i>arcticus</i>	70	114-157	136.2)	8.69	1.03	6.38

Table 15. Statistics of *Rangifer t. groenlandicus* Female Demes

Deme	n	Range	Mean	S.D.	S.E.	C.V.
BASAL LENGTH						
<i>groenlandicus</i>	6	283-300	289.8	7.78	3.18	2.68
<i>arcticus</i>	76	273-326	297.5	12.31	1.41	4.14
ORBITAL WIDTH						
<i>groenlandicus</i>	6	145-155	150.3	3.69	1.51	2.46
<i>arcticus</i>	76	142-159	149.8	4.20	0.482	2.80
NASAL LENGTH						
<i>groenlandicus</i>	4	92-97	95.0	2.16	1.08	2.27
<i>arcticus</i>	76	79-115	97.8	8.51	0.977	8.70
POST NARES						
<i>groenlandicus</i>	3	33.2-35.0	34.00	1.00	0.578	2.94
<i>arcticus</i>	70	30.5-38.5	34.23	1.81	0.216	5.62
TOOTH ROW						
<i>groenlandicus</i>	4	84.0-95.3	90.12	5.23	2.61	5.80
<i>arcticus</i>	76	78.3-99.0	88.71	3.92	0.450	4.42
DIASTEMA						
<i>groenlandicus</i>	3	104-108	105.6	5.10	2.95	4.83
<i>arcticus</i>	73	93-122	107.6	6.12	0.721	5.69
OCCIPITAL HEIGHT						
<i>groenlandicus</i>	3	118-123	122.0	3.61	2.09	2.96
<i>arcticus</i>	73	108-133	120.6	5.20	0.608	4.31

Table 16. Statistics of Nearctic Island Male Demes

Deme	n	Range	Mean	S.D.	S.E.	C.V.
BASAL LENGTH						
<i>cogroenlandicus</i>	4	264-290	275.0*	10.98	5.49	3.99
<i>pearyi</i>	64	279-343	304.6)	12.53	1.57	4.11
Banks Island.....	21	274-320	301.6)	13.92	3.04	4.62
ORBITAL WIDTH						
<i>cogroenlandicus</i>	8	139-157	147.75*	5.42	1.92	3.67
<i>pearyi</i>	65	145-169	157.7)	5.63	0.665	3.40
Banks Island.....	21	142-165	155.5)	5.88	1.28	3.79
NASAL LENGTH						
<i>cogroenlandicus</i>	8	81-97	86.75*	4.88	1.72	5.63
<i>pearyi</i>	65	81-120	98.8)	9.10	1.14	9.19
Banks Island.....	21	78-110	96.9)	8.82	1.93	9.10
POST NARES						
<i>cogroenlandicus</i>	3	31.5-36.3	34.07*	2.34	1.35	6.86
<i>pearyi</i>	61	31.6-42.4	35.65)	2.28	0.294	6.40
Banks Island.....	21	32.0-38.2	35.1)	1.34	0.293	3.81
TOOTH ROW						
<i>cogroenlandicus</i>	4	86.5-95.0	89.92)	3.56	1.78	3.96
<i>pearyi</i>	61	80.3-106	93.13)	5.30	0.684	5.69
Banks Island.....	21	85.8-98.0	92.55)	3.07	0.670	3.32
DIASTEMA						
<i>cogroenlandicus</i>	2	87-91	89.0*	2.83	2.01	3.18
<i>pearyi</i>	62	94-128	106.1)	6.33	0.804	5.97
Banks Island.....	21	94-115	105.1)	5.86	1.28	5.58
OCCIPITAL HEIGHT						
<i>cogroenlandicus</i>	4	104-137	120.5)	15.15	7.57	12.57
<i>pearyi</i>	63	117-152	129.1)	6.66	0.839	5.16
Banks Island.....	21	116-137	126.6)	6.63	1.45	5.24

Table 17. Statistics of Nearctic Island Female Demes

Deme	n	Range	Mean	S.D.	S.E.	C.V.
BASAL LENGTH						
<i>eogroenlandicus</i>	1		253			
<i>pearyi</i>	14	257-272	265.4	5.48	1.47	2.06
Banks Island.....	6	260-285	271.5	9.53	3.89	3.51
ORBITAL WIDTH						
<i>eogroenlandicus</i>	1		138			
<i>pearyi</i>	14	134-149	142.4	4.09	1.09	2.87
Banks Island.....	6	139-152	146.0	4.65	1.90	3.18
NASAL LENGTH						
<i>eogroenlandicus</i>	1		80			
<i>pearyi</i>	14	76-96	86.1	7.01	1.87	8.14
Banks Island.....	6	83-96	88.2	3.71	1.51	4.21
POST NARES						
<i>eogroenlandicus</i>	1		33.2			
<i>pearyi</i>	12	29.6-35.5	31.58	1.00	0.289	3.16
Banks Island.....	6	31.6-33.5	32.63	0.64	0.260	2.00
TOOTH ROW						
<i>eogroenlandicus</i>	1		79.50			
<i>pearyi</i>	12	78.0-93.0	87.69	8.20	2.37	9.35
Banks Island.....	6	84.7-89.8	87.40	1.90	0.775	2.17
DIASTEMA						
<i>eogroenlandicus</i>	1		92.0			
<i>pearyi</i>	12	86-93	90.5	3.91	1.13	4.33
Banks Island.....	6	89-100	95.2	4.22	1.72	4.43
OCCIPITAL HEIGHT						
<i>eogroenlandicus</i>	1		111			
<i>pearyi</i>	12	105-119	111.9	3.33	0.962	2.98
Banks Island.....	6	109-121	114.3	5.51	2.25	4.82

Table 18. Statistics of *Rangifer t. caribou* Male Demes

Deme	n	Range	Mean	S.D.	S.E.	C.V.
BASAL LENGTH						
<i>caribou</i>	19	338-388	361.6	14.19 12.33 9.75 13.94 19.68	3.25	3.92
<i>caboti</i>	23	342-396	374.6		2.57	3.29
<i>terraenovae</i>	12	343-375	365.0		2.82	2.67
<i>sylvestris</i>	32	357-427	377.1		2.47	3.70
<i>stonei</i>	26	345-421	384.3		3.78	5.12
ORBITAL WIDTH						
<i>caribou</i>	21	157-185	168.9 *	7.49	1.64	4.44
<i>caboti</i>	23	162-185	174.5	4.77	1.01	2.73
<i>terraenovae</i>	12	167-183	175.7	5.39	1.56	3.06
<i>sylvestris</i>	35	160-195	176.5	8.39	1.42	4.75
<i>stonei</i>	23	163-198	180.8	10.58	2.20	5.85
NASAL LENGTH						
<i>caribou</i>	21	117-155	134.0	10.85 10.57 12.79 12.15 11.88	2.37	8.10
<i>caboti</i>	23	122-163	134.0		2.20	7.89
<i>terraenovae</i>	12	115-162	(138.9)		3.70	9.20
<i>sylvestris</i>	35	111-151	129.0		2.05	9.42
<i>stonei</i>	25	103-148	126.6		2.38	9.38
POST NARES						
<i>caribou</i>	4	42.3-46.5	44.90	1.83	0.915	4.08
<i>caboti</i>	18	38.0-51.0	44.80	3.95	0.932	8.81
<i>terraenovae</i>	7	43.0-47.5	45.39	1.63	0.615	3.59
<i>sylvestris</i>	12	43.0-49.5	46.27	1.91	0.552	4.13
<i>stonei</i>	14	41.5-56.2	48.95	4.42	1.18	9.05
TOOTH ROW						
<i>caribou</i>	21	88.7-107	94.85	4.80 4.49 4.20 4.69 4.92	1.05	5.06
<i>caboti</i>	23	87.8-105	(97.39)		0.935	4.61
<i>terraenovae</i>	9	85.7-101	94.20		1.40	4.46
<i>sylvestris</i>	33	90.0-110	98.33		0.817	4.77
<i>stonei</i>	25	90.9-109	99.49		0.984	4.94
DIASTEMA						
<i>caribou</i>	21	125-148	136.4	8.56 7.20 4.44 7.83 10.62	1.87	6.27
<i>caboti</i>	23	128-154	(143.4)		1.50	5.02
<i>terraenovae</i>	12	128-147	138.1		1.28	3.21
<i>sylvestris</i>	31	126-164	137.9		1.41	5.68
<i>stonei</i>	25	127-166	143.3		2.12	7.41
OCCIPITAL HEIGHT						
<i>caribou</i>	12	132-162	146.1	8.21 8.08 6.80 12.05 13.64	2.37	5.62
<i>caboti</i>	23	135-168	147.9		1.68	5.46
<i>terraenovae</i>	10	147-164	155.3		2.15	4.39
<i>sylvestris</i>	31	131-188	159.0		2.16	7.58
<i>stonei</i>	23	132-181	162.1		2.84	8.41

Table 19. Statistics of *Rangifer t. caribou* Female Demes

Deme	n	Range	Mean	S.D.	S.E.	C.V.
BASAL LENGTH						
<i>caribou</i>	9	325-352	338.0	9.87	3.29	2.92
<i>caboti</i>	10	335-361	(343.8)	6.17	1.95	1.79
<i>terraenovae</i>	17	306-345	(321.4*)	12.72	3.09	3.96
<i>sylvestris</i>	19	307-368	332.3	13.98	3.21	4.21
<i>stonei</i>	10	332-362	341.3	8.56	2.71	2.51
ORBITAL WIDTH						
<i>caribou</i>	9	153-171	160.4	5.49	1.74	3.42
<i>caboti</i>	10	156-167	(162.3)	3.43	1.09	2.11
<i>terraenovae</i>	17	140-168	155.5	7.64	1.85	4.92
<i>sylvestris</i>	19	151-168	159.1	4.79	1.10	3.01
<i>stonei</i>	10	155-174	162.4	5.16	1.63	3.18
NASAL LENGTH						
<i>caribou</i>	9	112-130	117.2	8.04	2.68	6.86
<i>caboti</i>	10	115-139	126.2	7.43	2.35	5.89
<i>terraenovae</i>	17	100-136	118.0	10.10	2.45	8.56
<i>sylvestris</i>	19	92-143	114.4	15.33	3.52	13.39
<i>stonei</i>	10	95-119	110.4	7.54	2.39	6.82
POST NARES						
<i>caribou</i>	6	40.0-43.4	41.58	1.48	0.604	3.56
<i>caboti</i>	5	34.8-43.5	39.66	3.16	1.41	7.96
<i>terraenovae</i>	10	39.0-43.9	41.49	1.73	0.547	4.17
<i>sylvestris</i>	8	36.8-43.2	40.69	2.00	0.707	4.91
<i>stonei</i>	9	38.5-43.5	40.57	1.97	0.657	4.86
TOOTH ROW						
<i>caribou</i>	9	90.5-105	95.53	3.86	1.29	4.04
<i>caboti</i>	10	90.0-105	96.64	4.46	1.41	4.62
<i>terraenovae</i>	14	85.4-107	(91.95)	6.11	1.58	6.64
<i>sylvestris</i>	19	82.5-105	96.06	5.55	1.27	5.78
<i>stonei</i>	10	90.6-108	96.93	4.92	1.56	5.08
DIASTEMA						
<i>caribou</i>	9	119-139	126.8	5.81	1.94	4.58
<i>caboti</i>	10	121-135	(129.0)	5.01	1.59	3.88
<i>terraenovae</i>	14	117-133	119.3	7.61	2.03	6.38
<i>sylvestris</i>	14	108-135	121.9	7.62	2.04	6.25
<i>stonei</i>	10	119-136	127.5	5.80	1.84	4.55
OCCIPITAL HEIGHT						
<i>caribou</i>	7	127-138	132.3	5.29	1.76	3.40
<i>caboti</i>	10	122-147	134.0	7.27	2.30	5.43
<i>terraenovae</i>	14	115-143	127.8	8.43	2.25	6.59
<i>sylvestris</i>	17	113-147	129.0	10.71	2.60	8.30
<i>stonei</i>	10	133-147	138.6	3.59	1.14	2.59

Table 20. Statistics of Alaska-Yukon Demes: Males

Deme	n	Range	Mean	S.D.	S.E.	C.V.
BASAL LENGTH						
Nelchina.....	14	346-385	364.0	12.77	3.41	3.51
Yukon.....	4	344-374	364.7	13.91	6.95	3.81
Steese.....	3	349-362	353.7	4.18	2.42	1.18
Brooks Range.....	14	326-363	346.3	8.67	2.32	2.51
ORBITAL WIDTH						
Nelchina.....	14	163-183	173.9	5.28	1.41	3.03
Yukon.....	4	159-177	168.2	7.85	3.92	4.67
Steese.....	3	164-172	168.7	0.707	0.41	0.42
Brooks Range.....	14	162-174	167.6	3.40	2.03	0.909
NASAL LENGTH						
Nelchina.....	14	105-132	119.9	8.11	2.71	6.76
Yukon.....	4	107-132	117.2	11.18	5.59	9.54
Steese.....	3	106-113	107.7	1.41	0.82	1.31
Brooks Range.....	14	91-120	110.6	9.71	2.60	8.74
POST NARES						
Nelchina.....	12	42.0-50.4	44.71	2.00	0.54	4.47
Yukon.....	4	42.0-47.3	44.95	2.38	1.19	5.29
Steese.....	3	43.4-45.0	44.47	0.71	0.41	1.57
Brooks Range.....	10	37.2-42.6	40.25	2.16	0.68	5.36
TOOTH ROW						
Nelchina.....	14	84.2-105	94.14	6.75	1.80	7.17
Yukon.....	4	86.2-105	92.90	8.08	4.04	8.69
Steese.....	3	90.0-93.4	91.66	2.24	1.29	2.44
Brooks Range.....	14	84.2-93.6	89.86	2.70	0.72	3.00
DIASTEMA						
Nelchina.....	14	127-153	137.4	8.07	2.16	5.89
Yukon.....	4	130-149	140.2	9.22	4.62	6.59
Steese.....	3	130-141	134.3	6.92	4.00	5.15
Brooks Range.....	14	120-140	131.9	6.55	1.75	4.96
OCCIPITAL HEIGHT						
Nelchina.....	14	136-157	149.1	6.39	1.71	4.29
Yukon.....	4	141-159	152.2	8.06	4.03	5.30
Steese.....	3	136-148	143.0	7.00	4.05	4.89
Brooks Range.....	14	129-147	141.3	4.83	1.29	3.43

Table 21. Statistics of Alaska-Yukon Demes: Females

Deme	n	Range	Mean	S.D.	S.E.	C.V.
BASAL LENGTH						
Nelchina.....	10	328-361	339.9	11.63	3.68	3.42
Yukon.....	3	316-318	317.0	1.00	0.58	0.32
Steese.....	7	317-333	327.3	4.36	1.64	1.33
Brooks Range.....	6	301-323	308.8	9.02	3.68	2.92
ORBITAL WIDTH						
Nelchina.....	10	150-167	160.3	5.62	1.78	3.51
Yukon.....	3	153-156	154.3	4.24	2.45	2.75
Steese.....	7	152-167	158.7	6.23	3.35	2.92
Brooks Range.....	6	148-158	152.8	4.92	2.01	3.22
NASAL LENGTH						
Nelchina.....	10	105-132	114.9	7.67	2.42	6.66
Yukon.....	3	99-114	105.3	8.43	4.87	8.03
Steese.....	7	96-116	101.7	7.08	2.67	6.94
Brooks Range.....	6	82-114	98.3	10.84	4.42	11.03
POST NARES						
Nelchina.....	5	36.7-46.0	39.52	3.71	1.17	9.39
Yukon.....	3	36.8-45.9	40.57	4.69	2.71	11.5
Steese.....	7	38.0-43.5	40.40	1.87	0.71	4.63
Brooks Range.....	2	36.4-37.4	36.90	0	0	0
TOOTH ROW						
Nelchina.....	10	85.3-99.1	91.84	5.25	1.66	5.72
Yukon.....	3	90.7-92.8	92.00	1.22	0.71	1.33
Steese.....	7	83.9-99.2	90.69	5.73	2.16	6.32
Brooks Range.....	6	80.0-89.4	85.72	3.46	1.41	4.29
DIASTEMA						
Nelchina.....	10	120-141	128.2	6.96	2.21	5.45
Yukon.....	3	106-119	112.3	7.35	4.25	6.56
Steese.....	7	115-129	121.4	5.97	2.25	4.92
Brooks Range.....	6	112-122	116.8	4.92	2.01	4.21
OCCIPITAL HEIGHT						
Nelchina.....	9	128-145	137.1	5.96	1.89	4.35
Yukon.....	3	132-137	134.7	2.65	1.53	1.96
Steese.....	7	124-134	129.4	5.04	1.91	3.93
Brooks Range.....	6	118-128	123.7	1.67	0.68	1.35

Table 22. Coefficients of Correlation

Subspecies	Sex	Orbital Width/ Basal Length	Nasal Length/ Basal Length	Tooth Row/ Basal Length
<i>tarandus</i>	f.	.60638	.42974	.12809
	m.	.39706	.70909	.09947
<i>groenlandicus</i>	f.	.38206	.43709	.13588
	m.	.50678	.43079	.09920
<i>granti</i>	f.	.6874	.7904	— .4392
	m.	.00813	.68188	.29333
<i>pearyi</i>	f.	.16152	.8675	.9338
	m.	.77384	.55047	.16861
<i>cogroenlandicus</i>	f.	—	—	—
	m.	.841	.764	1.00
<i>platyrhynchus</i>	f.	.30139	.62502	.64514
	m.	.88678	.76575	.67141
<i>caribou</i>	f.	.72154	.41193	.29049
	m.	.69058	.29991	.73074
<i>fennicus</i>	f.	.61997	.83274	.2520
	m.	.51662	.68368	.39807

Table 23. Regression Line Equations for Males

Subspecies	Orbital Width on Basal Length	Nasal Length on Basal Length	Tooth Row on Basal Length
<i>tarandus</i>	$y = .199x + 98.1$	$y = .550x - 73.1$	$y = .0436x + 75.74$
<i>groenlandicus</i>	$y = .234x + 86.7$	$y = .299x + 5.4$	$y = .0317x + 80.86$
<i>granti</i>	$y = .00761x + 168.9$	$y = .830x - 170$	$y = .451x - 60.72$
<i>pearyi</i>	$y = .348x + 51.8$	$y = .396x - 21.5$	$y = .0713x + 71.41$
<i>cogroenlandicus</i>	$y = .415x + 33.5$	$y = .336x - 6.7$	$y = .324x + 0.76$
<i>platyrhynchus</i>	$y = .463x + 17.1$	$y = .512x - 58.0$	$y = .183x + 35.80$
<i>caribou</i>	$y = .353x + 43.5$	$y = .217x + 50.3$	$y = .217x + 16.28$
<i>fennicus</i>	$y = .248x + 86.0$	$y = .497x - 57.3$	$y = .130x + 47.41$

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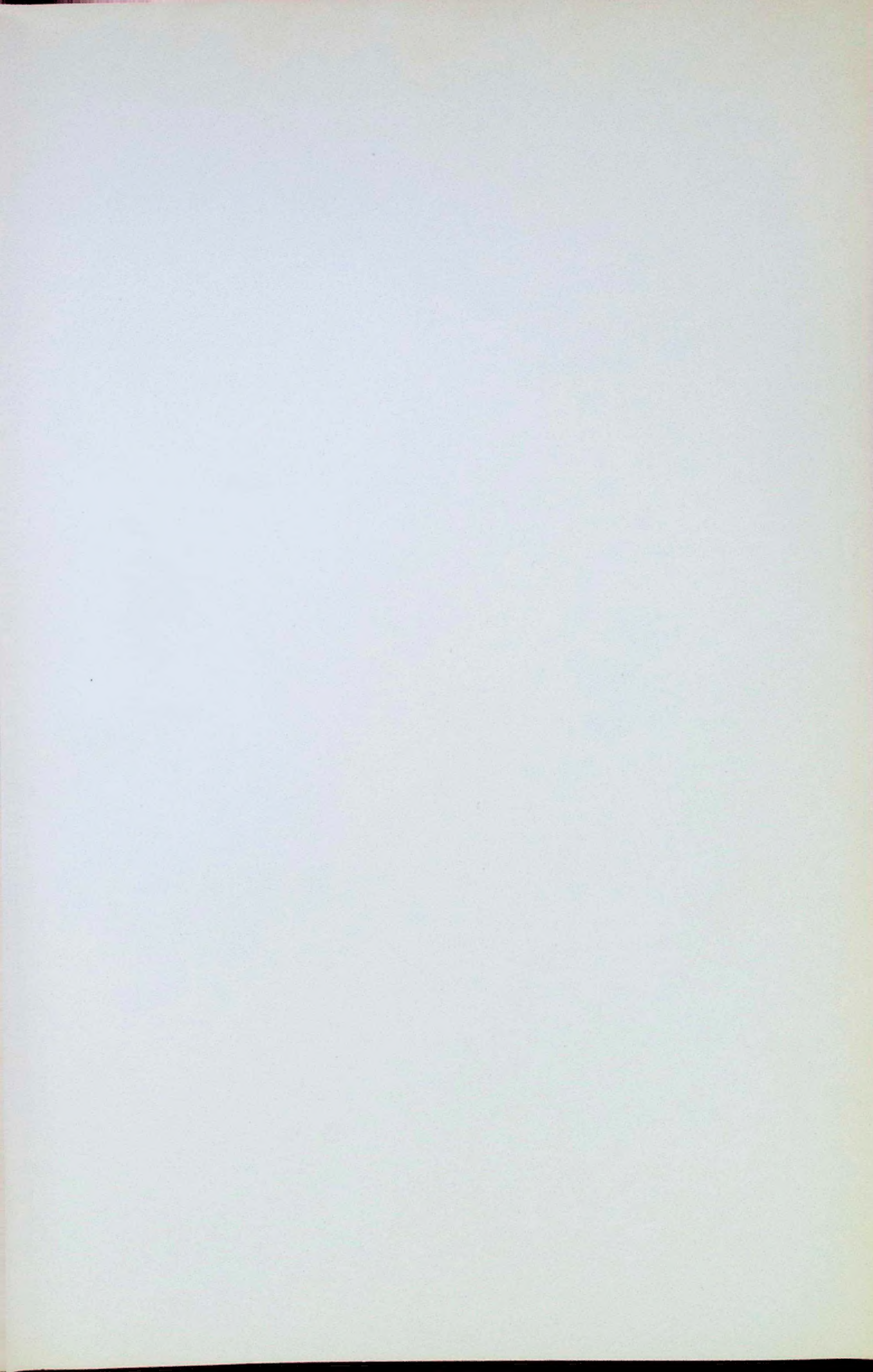
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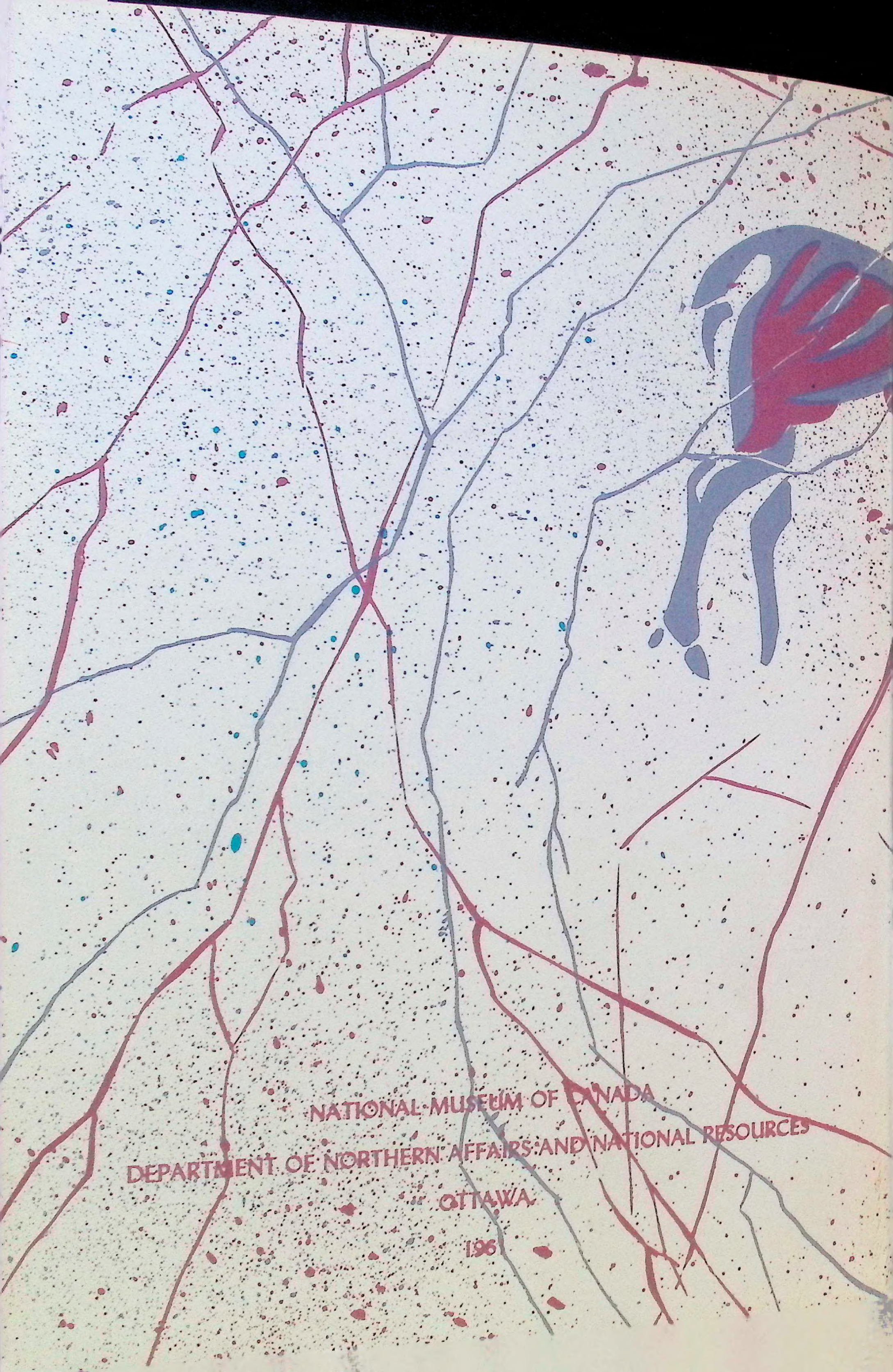
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